The Effects of Forest Management Practices on Forest Regeneration and Arthropod Diversity

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Summary

This PhD thesis investigates the effects of two major restoration methods that are currently being used to restore lowland dipterocarp forests throughout the Malaysian state of Sabah - Borneo. We examine the changes each treatment brings to the litter cycle, the growth and mortality of enrichment planted seedlings and to the canopy arthropod communities.

In chapter two, we monitor the difference in litterfall rates between the climber-cutting and the enrichment planting method. The climber cutting treatment aims on eliminating all all climbing plants in order to increase light levels to the forest floor and reduce below ground competition between targeted species. In this chapter, I show that the litter fall biomass increased by 130% in the short term (between 56 - 112 days). The litter fall volume then returned to control levels (Standard line planting method) at the end of the study period. The primary aim of this treatment to increase light levels to the forest floor had been successful by which canopy openness levels were on average increased by 47%.

In chapter three, we test the effects of the line planting and climber-cutting treatment on the growth and survival of 16 dipterocarp species. We monitored seedling growth over six time intervals from September 2009 to September 2013. On average the climber-cutting method increased seedling basal diameter growth rates (compared at a common size: size-specific relative growth rates (SGR) by 28%. All studied species showed an increased in growth rates in the enhanced climber-cutting method with the exception for one species (*Parashorea malaanonan)* which grew slower in the enhanced climber-cutting method while exhibiting higher growth rates (14%) in the line planting method.

In chapter four, we surveyed for canopy arthropods to monitor the changes the climber cutting treatment effects the population. We monitored changes in biomass as the treatment is implemented and found that four ordinal groups were affected by the climber-cutting treatment, Blattodea (cockroaches) showed an increase

in biomass by 388% and Hymenoptera - family: formicidae (ants), decreased by 45% in biomass when compared to pre-cutting (control) samples. Both groups (Blattodea and Hymenoptera - family: formicidae) did not return to control biomass volumes at the end of the study period (4 months post-treatment). Hemiptera (bugs) and Coleoptera (beetles) biomass increased by 31% and 59% respectively one month after treatment however, returned to control levels four months after treatment had been implemented. The remaining ordinal groups surveyed did not show any change in biomass.

To summarize we show that the treatment does not have major long term effects on the forest litter dynamics. Out of the 16 dipterocarp seedlings studied, one species showed negative performance in the climber cutting treatment. Out of all the arthropod ordinal groups sampled (20) two showed changes which were not stabilised by the end of the experiment. A resurvey both Blattodea (cockroaches) and Hymenoptera - family: formicidae (ants) is required to conclude the effects this treatment has on them.

Zusammenfassung

Diese Doktorarbeit untersucht die Wirkungen von zwei Rekultivierungsmethoden, die heute hauptsächlich eingesetzt werden, um Flachlandwälder mit Flügelfruchtgewächsen im Bundestaat Sabah in Borneo Malaysia wieder instand zu setzen. Wir untersuchen welche Folgen jeder Eingriff auf den Laubfall, auf das Wachstum und die Sterblichkeit von gepflanzten Setzlingen, sowie auf die Gemeinschaft von Gliederfüssern hat.

In Kapitel zwei vergleichen wir die Laubfallmengen bei der Anwendung des Schlingpflanzen-Schneidens oder der Anreicherungsbepflanzung in geraden Linien. Das Schlingpflanzen-Schneiden hat zum Ziel alle Schlingpflanzen von den Bäumen zu entfernen, damit mehr Licht auf den Waldboden trifft und die Konkurrenz zwischen den Arten im Boden zu verringern. In diesem Kapitel zeige ich, dass die Laubfallbiomasse kurzfristig um 130% gestiegen ist (zwischen 56-122 Tagen). Die Menge von Laubfall kehrte aber am Ende der Untersuchungszeit zu verlgeichbaren Mengen wie in den Kontrollgruppen (Anreicherungsbepflanzungsmethode) zurück. Nach der Anwendung des Schlingpflanzen-Schneidens war das Blätterdach durchschnittlich 47% offener als vorher, somit wurde das primäre Ziel dieser Methode erfolgreich erreicht: Mehr Licht auf dem Waldboden.

In Kapitel drei untersuchen wir die Wirkungen der Anreicherungsbepflanzung und das Schlingpflanzen-Schneiden auf das Wachstum und das Überleben von 16 Flügelfruchtgewächsarten. Wir beobachteten das Wachstum von Setzlingen zwischen September 2009 bis September 2013 in 6 Zeitintervallen. Im Durchschnitt erhöhte die Schlingpflanzen-Schneidemethode die Wachstumsrate des basalen Setzlingdurchmessers um 28% (korrigiert mit der grössenspezifischen relativen Wachstumsrate (SGR)). Alle untersuchten Arten zeigten eine Zunahme der Wachstumsrate bis auf eine (*Parashorea malaanonan)*, welche langsamer wuchs mit der Schlingpflanzen-Schneidemethode, aber eine höhere Wachstumsrate (14%) aufwies mit der Anreicherungsbepflanzungsmethode.

In Kapitel vier untersuchen wir die Wirkungen der Schlingpflanzen-Schneidemethode auf die Gemeinschaften von Gliederfüssern im Blätterwerk. Wir fanden heraus, dass die Biomasse von vier Ordnungen durch die Schlingpflanzen-Schneidemethode beeinflusst wurden. Blattodea (Schaben) zeigten einen Biomassenanstieg von 388% und die Hautflüglerfamilie Formicidae (Ameisen) eine Biomassenabnahme von 45% im Vergleich zu Kontrollen vor der Anwendung der Methode. Beide Gruppen (Schaben und Ameisen) kehrten auch nicht am Ende der Untersuchungsperiode (4 Monate nach dem Eingriff) zu den Kontrollbiomassewerten vor der Anwendung der Schlingpflanzen-Schneidemethode zurück. Die Biomasse von Hemiptera (Schnabelkerfe) und Coleoptera (Käfer) stieg zwar einen Monat nach dem Eingriff um 31% bzw. 59% an, kehrte aber nach vier Monaten zu den Kontrollwerten von vor dem Eingriff zurück. Alle anderen untersuchten Ordnungen zeigten keine Änderungen in der Biomasse.

Zusammenfassend zeigen wir, dass die Schlingpflanzen-Schneidemethode keine wichtigen Langzeiteffekte auf die Laubfalldynamik des Waldes hat. Von den 16 untersuchten Flügelfruchtgewächsarten zeigte eine Art negative Effekte bei der Anwendung der Schlingpflanzen-Schneidemethode. Von allen erfassten Gliederfüsserordnungen (20) kehrten zwei auch am Ende des Experiments nicht zu ihren ursprünglichen Werten zurück. Eine weitere Untersuchung der Ordnung Blattodea (Schaben) und der Hautflüglerfamilie Formicidae (Ameisen) ist nötig, um schlüssig zu folgern, welchen Einfluss die Methode auf diese zwei Gruppen hat.

Chapter 1: **General Introduction**

General Introduction

Tropical rainforest are considered one of the most diverse terrestrial regions. Ranging from 23 °N to 23 °S, they are estimated to hold two-thirds of the world's flowering plant diversity, comprising of around 170,000 species (Whitmore 1998). Estimates of fauna diversity vary from two to three million species of which a large percentage is composed of insects (Whitmore 1998). Globally forests are important for the maintenance of a range of ecosystem services, including the regulation of global gaseous composition, generation and maintenance of soils and the control of regional climatic conditions (Chazdon 2008, Noble & Dirzo 1997, Bonan 2008). Throughout Southeast Asia, roughly 63% of the total remaining forest is dominated by logged over and degraded forests (Kettle 2010). In the Malaysian states of Sabah and Sarawak on the island of Borneo, 80% of land coverage has been affected by logging operations between 1990 and 2009 (Bryan et al. 2013). Intact forest in the state of Sabah is confined to protected areas that make up 8% of total land cover leaving a large proportion of logged over forests. Forests subject to selective logging are often valued less (in terms of retaining biodiversity and ecosystem functioning) compared to their primary states. However, logged over forests are capable of retaining high levels of floral and faunal diversity (Edwards et al. 2011, Berry et al. 2010, Woodcock et al. 2011) and efforts to regenerate and conserve these forests have gained a large conservation momentum.

Lowland Dipterocarp forests

The tropical forests of South-East Asia are dominated by a family of tree: the Dipterocarpaceae. The dipterocarps consists of over 470 species, of which 270 occur on the island of Borneo (Ashton 1988). This family of tree makes up 80% of canopy trees and 40% of understory individuals (Mabberley 1992). On average, dipterocarps reach 45m in height with emergent species capable of reaching heights above 60m (Whitmore 1984). The reproduction process of dipterocarps is triggered by drought (Kobayashi et al. 2013) which during an El Niño–Southern Oscillation (ENSO) causes a synchronous, supra-annual mass fruiting event at a community-level referred to as masting or general flowering (Sakai et al. 2006, Appanah 1993). Seeds of dipterocarps are recalcitrant and germinate between 2-13 days (Appanah & Turnbull 1999). The masting event creates seedling stocks that are generally dispersed close to the parent tree due to the poor dispersal of dipterocarp seeds (Itoh et al. 2003). There has been a large amount of hypotheses in the past

which attempt to explain the ecological significance of the mass fruiting event, including predator satiation (Janzen 1970, Silvertown 1980, Connell & Green 2000), the increased in pollination efficiency (Smith et al. 1990), accumulation of reserves during non-reproductive periods (Sork 1993), and favorable conditions after ENSO events which increases drought occurrence and tree mortality that creates an increased amount of gaps creating favorable conditions for seedlings to grow (Curran et al. 1999, Yasuda et al. 1999, Williamson & Ickes 2002).

Logged over lowland tropical forests

Forestry products such as timber are an important source of revenue for many countries in South-east Asia. During the end of the 20th century, Indonesia, Malaysia and the Philippines contributed to 80% of all tropical timber produced. In 2006 an estimated USD 39 Billion was generated by logging activities from this region (Miles & Kapos 2008). In the Malaysian state of Sabah (island of Borneo), almost all of its states commercial forests cover have been logged once and in some cases re-logged, leaving a large area of degraded forests (Reynolds et al. 2011).

Logged over forests currently dominates a large percentage of forested land. Although often termed degraded forest, these forests are capable of retaining a large percentage of diversity. Selective logging predominantly affects stocks of aboveground biomass with an estimated loss of 53% after a harvest operation (Berry et al. 2010). However despite this loss, studies comparing logged over forest with primary forests show that these forests are still capable of retaining 90% of plant species (Berry et al. 2010) with over 75% avian and dung beetle (Edwards et al. 2011) and 80% of ant diversity retained (Woodcock et al. 2011).

Lianas and climbing plants

Woody vines or climbers (lianas and climbing bamboo) are structural parasites of trees. Climbers trade off structural investment of supporting themselves and invest in vertical growth (Stevens 1987) where they use the architecture of trees to ascent to the canopy (Schnitzer & Bongers 2002). Lianas are highest in abundance in the tropics (Schnitzer & Bongers 2002), where they contribute up to 40% of woody stem densities and more than 25% of plant diversity (Gerwing & Farias 2000, Chave et al. 2001). In tropical forests, lianas contribute to forests production and are responsible for up to 20% of leaf productivity (Phillips et al. 2008).

Lianas play important roles in forest dynamics, where they are known to suppress tree regeneration and increase tree mortality(Putz 1984, Clark & Clark 1990), provide vital food sources for animals and increase connectivity between trees, improve tree-to-tree networks for arboreal animals (Putz 1991).

Liana densities show a high level of variation among sites where densities vary between 44% (Ibarra-Manriquez & Martinez-Ramos 2002) to as low as <10% of woody species (Appanah et al. 1993) where they are seen to be at highest densities in gaps (Hegarty & Cabelle 1991). There are many factors affecting their densities such as total rainfall, high seasonality of rainfall, soil fertility and forests disturbance (Schnitzer & Bongers 2002). A study carried out in Sabah, Malaysian - Borneo, found that lianas infested nearly 70% of all trees (>20 cm in diameter) in logged forests, where else in primary forests the study found that only 41% of trees (>10 cm diameter) were vine infested (Campbell & Newbery 1993). A high variation also occurs between shade-tolerant (late successional) trees and pioneer (early successional) trees, where Clark and Clark (1990) found that <1% of pioneer trees hosted lianas as compared to late successional trees, which almost all hosted lianas.

However in recent times, liana densities have been on the rise. Long term studies in the Amazon have found that over the last two decades of the 20th century, liana dominance over large trees have been in an increase from 1.7% to 4.6% (Phillips et al. 2002). Many theories attempt to explain this increase in dominance including; increasing evapotranspirative demand (Schnitzer 2005), large scale disturbance and turnover such as logging (Pinard & Putz 1994) and the increase in atmospheric carbon dioxide (Granados & Körner 2002).

Implications for future species composition

There has been a growing concern with the increase in dominance of lianas in tropical regions. Predominantly the largest concerns include how their increasing densities will affect community composition and ecosystem level dynamics, the removal of climbing plants in a large scale will also contribute to these changes. It has now already been established that lianas affect trees in terms of decreasing tree diversity, recruitment, growth and survival in both intact forests and in tree fall gaps. Furthermore, the largest concerns will arise as studies have shown that lianas effect later successional trees more than pioneer trees (see: (Clark

& Clark 1990)).

The rise of atmospheric carbon dioxide increases the growth rates of lianas (Granados & Körner 2002) putting lianas in a competitive advantage because of traits such as; having higher ratio of leaf area to total plant mass (LAR) (Cai et al. 2009), higher specific leaf area (SLA) and photosynthetic rates, high photosynthetic nitrogen and phosphorus use efficiency and lower leaf construction costs and leaf life span (Zhu & Cao 2010) which all contribute to faster growth rates compared to trees with rising atmospheric CO_2 (reviewed by (Schnitzer & Bongers 2011)). With these traits causing an increase in liana densities, forest whole carbon uptake might be greatly reduced as liana abundance increases causing an increase in tree mortality and reducing tree growth (Van Der Heijden et al. 2010, Ingwell et al. 2010) which in turn can cause an overall decrease in whole forests CO_2 uptake. This unequal competition may be an important driver for shifts in tree species coexistence (Körner 2006).

Efforts to Regenerate tropical forests

Climbers and woody vines have long been managed by land managers who have included pre-felling silvicultral management of vines in order to reduce forest gaps caused by the felling of trees (Pinard & Putz 1994). However, with large amounts of logged over forests and with increasing efforts to regenerate these forests, post-logging management by the mechanical cutting of climbing plants (hereby referred to as climber-cutting) has become a major method used to regenerate these forests. Early liana removal experiments have shown that lianas reduce tree growth and fecundity via above-ground and below-ground competition (Whigham 1984, Stevens 1987). Studies carried out in Panama have shown that the removal of lianas improved tree growth by 55%, recruitment by 46% and species richness by 65% (Schnitzer & Carson 2010).

Although the cutting of lianas as a management strategy because of poor felling management is costly (Pérez-Salicrup et al. 2001), the climber-cutting method is still carried out extensively as an alternative to enrichment planting. Enrichment planting is a reforestation method carried out where no or a limited amount of viable stocks of desired trees or seedlings persist (Chan et al. 2008). The enrichment planting method of

forest regeneration includes the restocking of forests by planting seedlings and clearing competing neighboring plants on the ground level. In the Malaysian State of Sabah (on the island of Borneo), the climber-cutting method has been carried out vastly, covering areas of 130,351 hectares of forest from 2006 to 2007 and has gained popularity among forest managers for its cheaper application costs when compared to enrichment planting (Sabah Forestry department, unpublished).

However there are many unknown factors which have not been considered to our knowledge. Studies in the past (carried out in South America) have looked predominantly on how this treatment effects plant performance and diversity however have not considered effects such as the cycling of litter fall and changes it causes to arthropod communities. On one hand the treatment may be beneficial towards the seedlings however the consequences for organisms dependent on lianas and climbing plants have not yet been investigated. Lianas provide extensive amount of connectivity among canopy trees and are capable of increasing habitat space useful for canopy arthropods. Lianas are important food sources for primates and birds as some species fruit outside on a regular basis (every year). The wide scale elimination of lianas may cause disruption that has yet to be quantified.

Arthropod diversity

Arthropods contribute to a large proportion of the faunal biomass in tropical systems (Basset et al. 2012) and play an important role in ecosystem functioning (Janzen 1987). Arthropods are responsible for services that include plant pollination, maintenance of species by herbivory and soil production by decomposition. In tropical rainforest ecosystems, arthropods are vertically distributed (Dial et al. 2006), where the forest canopy layers provide an abundance of habitats for which arthropod communities survive. Epiphytic plants play a major role in supporting this level of diversity where large percentages of arthropods use these structures as nesting sites (Ellwood et al. 2002). Lianas and climbing plants contribute to the connectivity of these arboreal habitats where they provide linkages between canopy trees and are often used by ants (Yanoviack 2012). A study by Snaddon et al. (2012) looking at removing habitat complexity (by the removal of arboreal marasmiod fungi) has illustrated that 70.2% of arthropod abundance was loss. While the manual eradication of climbing plants using the climber-cutting method is intended to increase canopy openness its

effects on arthropod communities have yet to be quantified.

Aims and hypotheses

In this thesis, I examine the effects of two major reforestation methods on forest dynamics such as leaf litter production and cycles, canopy dynamics, seedling growth and survival and the effects it has on arthropod communities. Specifically I will be testing the hypothesis that: 1) Managing forests by the climber cutting silvicultral treatment will produce higher levels of litter and canopy openness as compared to the enrichment planting method; 2) litter fall volumes will fall below control levels once woody vines have been cleared; 3) dipterocarp seedlings show differences in response rates in different restoration method (including investigating if dipterocarp seedling traits play an important factor in predicting the ability of seedlings to respond positively (high growth/low mortality) to the climber cutting treatment); 4) does the eradication of climbing plants effect habitat space and cause a decrease in arthropod biomass; and finally 5) does arthropod communities return to natural (control) volumes once the treatment effect has taken place.

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Chapter 2: **Changes in litter fall and canopy dynamics of highly managed lowland dipterocarp forests of Borneo**

Changes in litter fall and canopy dynamics of highly managed lowland dipterocarp forests of Borneo

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Abstract

In degraded tropical forests of Sabah, Malaysia, active restoration strategies have been adopted to enhance forest recovery rates above the natural level. To increase light conditions for both naturally occurring and enrichment planted seedlings on the forest floor, elimination of woody climbers such as lianas and climbing bamboo, have been implemented over large areas (130, 351 hectares from 2006 to 2011). However the removal of these climbers may cause unintended changes in litterfall dynamics that may cause disruption in the nutrient cycle, soil water content and affect soil respiration. Such changes can have negative impacts on soil biodiversity and could also cause an increase of CO_2 release into the atmosphere. In this study we examine the effects of liana and bamboo cutting (climber cutting treatment) and evaluate their impacts on the litter cycle. We compared two forest restoration treatments: (1) standard line planting (LP) and (2) line planting with enhanced climber cutting (ECC). Changes in canopy coverage and litterfall rates were measured over a one year period. We found that the ECC method increases overall litter fall by 130% in the short term (between 56 to 112 days) and annually this treatment increased litter production volume by 17% in comparison to the standard LP method. The ECC method increased understory light conditions by 47%. After a period of one year, the treatment did not cause any long-term changes in the litter cycle. The ECC treatment shown from our findings suggest that the primary aims of increasing light conditions can be achieved in a short period of time however causes a disruption to fruit and flower production where we found the treatment to reduce annual fruit and flower production by 81%.

Introduction

Tropical forests are among the most species rich terrestrial systems, forests are important for the maintenance of a range of ecosystem services, that includes the regulation of the global gaseous composition, generation and maintenance of soil and the control of regional climate (Chazdon 2008, Noble & Dirzo 1997, Bonan 2008). A single hectare of forest in Borneo is estimated to contain as many as 300 species of trees (dbh ≥ 1 cm) with average densities reaching 6,000 individuals (Gentry 1988, Losos & Leigh 2004). However, over recent decades tropical forest have been over exploited and replaced by a series of threats including logging and are often subsequently converted for agricultural purposes (Marsh 1992, Koh & Wilcove 2008, Carlson et al. 2012). Here we investigate how intensively rehabilitating degraded forest changes the dynamics of litter production and canopy openness.

The lowland tropical forest of Borneo is largely dominated by a single family of trees: the Dipterocarpaceae, with around 270 species occurring in the Malaysian state of Sabah (Ashton, 1982). This family of trees represents 25% of stems (120 stems ≥ DBH 10 cm ha^{-1}), with larger trees contributing to 70-80% of the canopy / emergent trees and contributing to half (15 m^2 ha^{-1}) of the total basal area (Whitmore 1984, Appanah 1993, Sist & Saridan 1999). The slow regeneration biology of this family (Sist et al. 2003) coupled with the high value of its timber, have left these forests with little economic value after repeated cycles of selective logging. However, these degraded forest are still a valuable refuge for a range of organisms and are capable of maintaining high levels of biodiversity after logging. Studies by Edwards *et al*. (2011) showed that logged forests have been able to sustain up to 75% of both dung beetle and avian diversity compared to primary forests. A meta analysis carried out by Berry *et al*. (2010) found floral diversity to be higher in logged forest. However their value for residual biodiversity is often not incorporated or considered when these degraded forest are converted for agriculture use. A study by Koh and Willcove (2008) has shown that from 1990 to 2005, 55 to 59% of oil palm expansion in Malaysia and Indonesia increased at the cost of forests.

Recently forest regeneration schemes such as the United Nations financial mechanism Reducing Emissions from Deforestation and Forest Degradation (REDD and REDD+), have influenced the potential economic

value of primary forest and efforts to restore degraded tropical forests throughout South-east Asia. This financial mechanism aims at crediting entire nations for their achievements in reducing carbon emissions from avoided deforestation (Miles & Kapos 2008). In Sabah, alternative reforestation projects such as 'Biodiversity Banking' (Bekessy & Wintle 2008) have successfully increased the protection status of 34,000 hectares of logged over forest by the sales of 'biodiversity credits' to corporations and individuals, for example the Malua BioBank (Malua Biobank, 2013).

Forest restoration techniques vary depending on the degradation level and the desired outcome of each project (Chazdon 2008). Once repetitively logged, large areas of lowland Dipterocarpaceae forests become highly susceptible to liana and vine infestation due to the extensive opening of the forest canopy (Cleary et al. 2009, Pinard & Putz 1994). Lianas are known to be structural parasites to trees (Stevens 1987) where they trade off investing in structural growth to vertical growth in order to reach the forest canopy (Gilbert et al. 2006). Lianas have been found to negatively affect forests dynamics and function (Schnitzer et al. 2012) with various studies showing that lianas reduce tropical tree recruitment, growth, survival and diversity (Putz 1984, Schnitzer et al. 2000, Schnitzer & Carson 2010). In more recent times the increased levels of atmospheric carbon dioxide have shown to caused an increased in liana dominance seen throughout forests of South America (Heijden et al. 2008, Phillips et al. 2002, 2008, Körner 2004, Granados & Körner 2002). Active restoration of degraded forests have been taking place in Sabah from as early as 1992, with the INFRAPRO project which covers an area of approximately 30,000 hectares. According to the Sabah Forestry department's annual reports, 17,490 hectares (from 2007 to 2011) have been restored by enrichment planting and 130,351 hectares (from 2006 to 2011) have been treated with silvicultural methods such as the cutting of climbing bamboo and lianas (climber cutting). In Sabah, the climber cutting method has been regularly applied as a silvicultural treatment in order to enhance the growth rate of remnant targeted tree species (primarily Dipterocarpaceae). The climber cutting method has been increasingly used in forest that contains sufficient stocks of Dipterocarps and used more often as a cheaper alternative to enrichment planting (Pérez-Salicrup et al. 2001). This restoration technique aims to improve light conditions for seedlings but may produce unintentional changes in litter fall dynamics.

Light remains as one of the limiting factors for growth of seedlings on the forest floor (Grubb & Burslem 1998, Whitmore et al. 1993). On average temperate and tropical forests with intact canopy receive as little as <2% photosynthetically active radiation (PAR) to the forest floor. Shade house experiments of 21 species of Dipterocarps have shown that higher light levels (18%), increases growth rates (Philipson et al. 2011) and manipulations of light conditions by liberation thinning methods (tree girdling) have been found to increase growth significantly (Kammesheidt et al. 2003). However the manipulation of light conditions by climber elimination could cause beneficial short-term increase in light levels to the forest floor but detrimental long-term changes in litter fall dynamics. Litter fall represents a major process for the transfer of nutrients from above to below ground (Vitousek & Sanford 1986, Attiwill & Adams 1993) and is often closely correlated with soil respiration (Raich & Nadelhoffer 1989, Davidson et al. 2002). In South America, litter manipulation studies carried out in lowland semi-evergreen tropical forest in Panama (Sayer & Tanner 2010) and tropical lowland forests in Costa Rica (Wood et al. 2009) have both shown that an increase in litter has a positive effect on soil nitrogen (N) and phosphorus (P) levels. Differences in litter quantity and quality have also been shown to cause changes in composition and abundance of soil fauna and microbial communities (De Deyn & Van der Putten 2005). Woody climbers such as lianas are important contributors to litter, where they contribute approximately 20% to forest leaf productivity (Phillips et al. 2008). The elimination of climbers could change the long-term dynamics of litter fall, and thus reduce the total amount of litter by 20%.

Here we investigate litter fall dynamics and changes in canopy openness over a year in a large-scale forest restoration experiment in northeast Borneo. This study compares litter fall rates and changes in canopy openness in two commonly used restoration techniques: line planting (LP) and enhanced climber cutting (ECC) (Chan et al. 2008). The objective of this study is to investigate the changes in litter fall volume and composition prior to and following ECC treatments. We are interested in understanding the duration of the effect of the climber cutting treatment on litter fall dynamics and how much this treatment changes canopy conditions. We hypothesize that: (1) the ECC restoration method will have higher levels of litter and canopy openness following treatment; but (2) litter fall volume will fall below natural levels once treatment effect has completely taken place.

Methods

STUDY SITE - This study was conducted for one year from May 2011 to June 2012 in a large scale forest restoration experiment: The Sabah Biodiversity Experiment (05°05'20" N, 117° 38'32" E) located 65 kilometers along the main logging road from the Danum Valley Field Centre (4°58'49" N, 117°51'19" E) in the Malaysian state of Sabah, Borneo (Figure 1). Forest in this region is classified as lowland mixed dipterocarp forest. The Malua forest reserve that the experiment is based within was selectively logged during the early 1980s. The surrounding reserve was then consecutively re-logged in 2007 with the exclusion of the study site. Pre-logging volume of trees was estimated at 193 - 221 m^3 ha^{-1}, from the total, 180 - 216 m^3 ha^{-1} composed of dipterocarps (Hector et al. 2011).

Annual precipitation recorded at the field station averaged at 3000 mm / year (Hector et al. 2011), with rainfall during the duration of the experiment (2011) reaching 3603 mm, with an average temperature of 25.5°C. Soil in the region is characterised as orthic acrisol (pH < 6) with a base saturation of 81 percent (Hector et al. 2011).

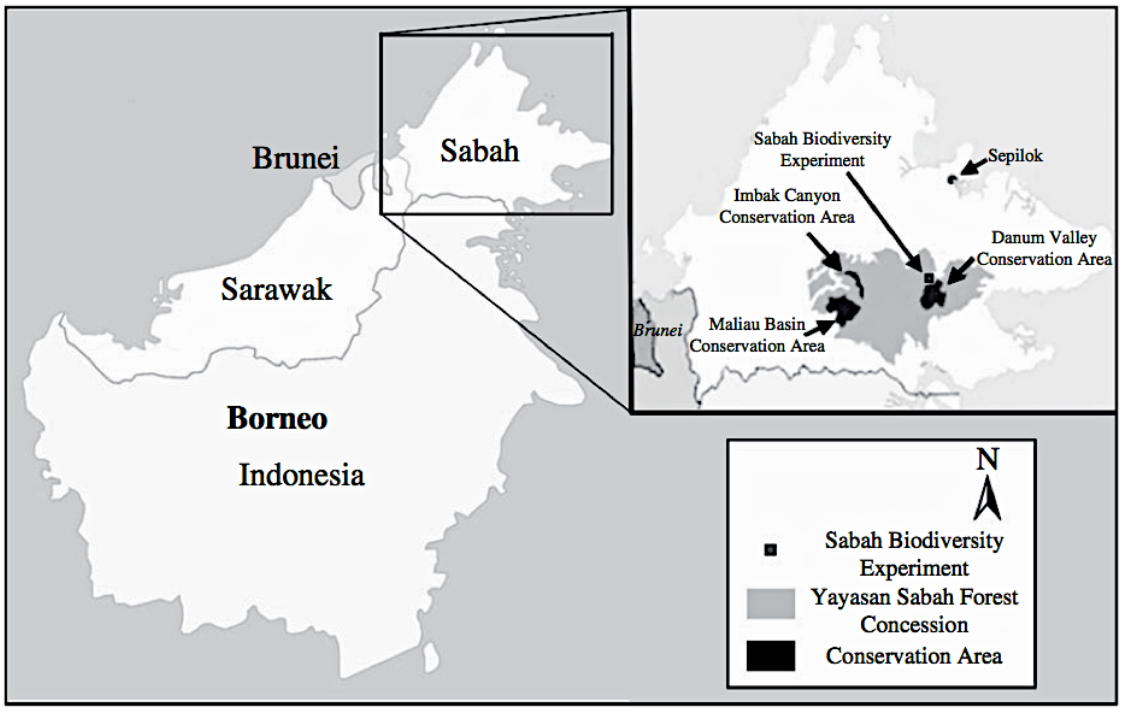

FIGURE 1: Location of study site in the Malaysian state of Sabah, Borneo (Hector et al. 2011).

EXPERIMENTAL DESIGN - Litter collection transects were set up within the Sabah Biodiversity Experiment, see: Hector *et al*. (2011) for the detailed experimental design. Experimental plots were divided into two main treatments: (1) standard line planting (LP) method (in this study used as a control) (200 x 200, n=7) and (2) enhanced climber cutting (ECC) treatment (200 x 200, n= 7). Standard LP methods consist of 200 m long planting transects with 3 m wide planting strips, consistent with the standard rehabilitation method widely used in Malaysia (Chan et al. 2008). All understory herbaceous plants were cleared manually from the 3 m wide planting strips. Parallel 200 m long planting transects run in a north to south direction and separated every 10 m apart. Each experimental plot consists of 20 planting lines. ECC plots consisted of standard LP methods with an additional treatment in which all climbers (lianas and climbing bamboo) >1 cm diameter was manually eradicated. Experimental plots were planted in 2003 and repeated in 2011 with a mixture of 16 canopy tree species belonging to the Dipterocarpaceae family. The selection of species was based on seedling availability during the set up of the experiment (2003) and natural occurrence of the species in similar forest type (Refer to chapter three for full list of species).

LITTER FALL SAMPLING - Four 1 m^2 (1 x 1 m) litter fall traps were established in each selected plot (n=14) in May 2011. As a control, litter fall traps were placed 2 months before treatment implementation to compare plot difference in litter fall rates. Four litter collection trays were placed in the stabilised of selected plots and separated every 10 meters in an east to west direction. Litter fall was collected every two weeks from 14 selected plots (n=54) from 13 May 2011 to 14 June 2012. Litter fall traps were constructed using PVC piping and fine mesh and suspended 1.3 meters above the forest floor to avoid disturbance by animals. Litter fall traps were suspended by attaching traps to neighboring vegetation and stabilised using wooden poles. Litter samples were dried for a period of seven days in a solar drying room, before being oven dried at 65°C for 48 hrs. Dried litter was separated into leaves, woody tissues, reproductive parts and miscellaneous materials (unidentifiable plant parts) prior to being weighed.

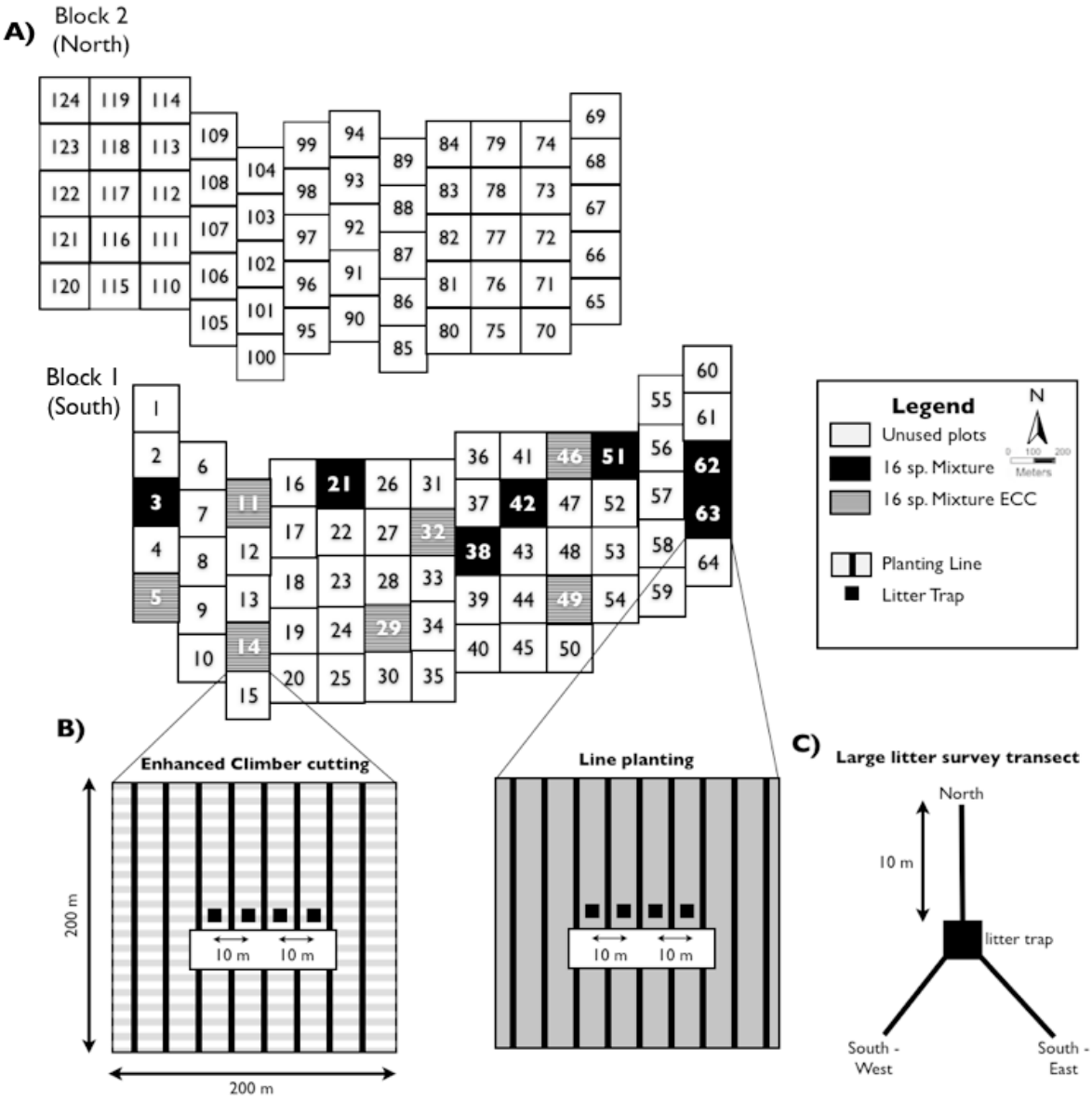

FIGURE 2: Layout of the experiment site (Sabah Biodiversity Experiment) with; (A) selection of plots within the SBE (n=14); (B) Litter trap layout and location within plots; (C) position of large litter survey transects from litter traps.

LARGE LITTER TRANSECTS - At each litter trap, 10 m transects in three directions were established (north, south-east, and south-west (Figure 2C)). Woody tissue longer then 1 m in length or ≥2 cm in diameter that fell within the transect line were surveyed. Large litter fall transects where established from 13 May 2011 and surveyed on a monthly basis. Length, diameter and decay level (scale of 1-5) of each woody tissue (see Table 1).

TABLE 1: *Large litter fall decay scale*

Litter decay scale	1	2	3	4	5
Wood appearance	Wood freshly fallen with core green/ brown	Wood no longer hard and dents if pressed	Wood soft and easily damaged when pressed	Wood fragile, crumbles when handled	Wood no longer circular, partially decomposed to soil

ENHANCED CLIMBER CUTTING TREATMENT - The ECC treatment was implemented from 8 July 2011 - 23 July 2011. Three teams of two field staff members cut all woody vines including climbing bamboo (*Dinochola* spp.) and lianas larger then 1 cm within experimental plots. Bamboo and liana densities (>1 cm diameter) within each plot were estimated using counts of sprouting stems cut.

CANOPY AND FOREST VARIABLES - Canopy coverage above each trap was estimated with a spherical densiometer (Lemmon 1956) every month for the duration of the experiment. Canopy height measurements were estimated with the use of a clinometer (Suunto PM-5/360 PC) at six points at 50 m intervals along two randomly selected planting lines within each plot. Basal area was also estimated at six 50 m intervals using the variable — radius plot (point sampling) method (Avery 1975, Bitterlich 1984). Prism sweeps were carried out using prisms with a 10 m^2 ha^{-1}.

DATA ANALYSIS - Differences in litter fall, large litter fall and canopy cover between different restoration strategies were analysed using mixed effects models: 'lme4' package version 0.999375-42 (Bates & Maechler, 2010) using the software package R (version 2.15.0: R. Core Development Team 2012). In all analysis, treatments were analysed as fixed factors and plot, litter trap and measurement interval were included as random factors. The best model of litter fall rates and difference in canopy openness was selected using a stepwise procedure retaining model terms based on Akaike's Information Criterion (AIC).

Results

LITTER FALL COMPOSITION - Annual total litter fall was higher in the ECC treatment compared to the LP method (table 2). Litter fall composition on average was dominated by leaves (72%), woody tissue (17%), reproductive parts (0.2%) and miscellaneous materials (11%). Leaves and woody tissue were higher in the ECC plots (table 2). Reproductive parts however, were higher in the LP treatment (table 2). No significant difference was seen between the two treatments for the production of miscellaneous materials (table 2).

Litter fall volume in ECC plots peaked two weeks (day 70) after treatment implementation began (Figure 3a). Leaf litter (figure 3b) contributed to the overall total trend of litter-fall pattern post treatment. All remaining components of the litter-fall composition with the exception of reproductive parts showed an increase in production between collection days 140 - 164 (Appendix 1c and 1e). Total litter fall production in ECC plots and LP plots was seen to increase for a second time during the 126 to 140 day sampling period (September to October) (Figure 3a).

TABLE 2: *Annual litter fall production per meter (± SE) by litter components between May 2011 to June 2012 .*

Component (g/m²/ year)	Line planting	Enhanced climber cutting	NumDF	DenDF	F	P
Total	724.70 ± 32.01	851.35 ± 32.01	1.0	11.9	14.1	0.003
Leaves	556.67 ± 27.73	617.41 ± 27.73	1.0	11.9	4.9	0.05
Reproductive parts	3.3586 ± 0.7581	0.6243 ± 0.7581	1.0	1257	5.4	0.02
Woody tissue	95.59 ± 16.59	147.04 ± 16.59	1.0	11.9	5.33	0.04
Miscellaneous	66.602 ± 9.043	84.308 ± 9.043	1.0	11.8	2.14	0.2

LITTER FALL STABILISATION - A difference of 130% in litter volume was observed between ECC plots and LP plots directly after treatment implementation (Figure 4). There was a significant difference between both treatments ($F_{1,11}$= 30.7, P<0.001). A significant decrease in litter fall rates was seen post treatment ($F_{1,11}$= 17.7, P<0.001). Increased litter fall rates produced by the ECC treatment returned to standard LP

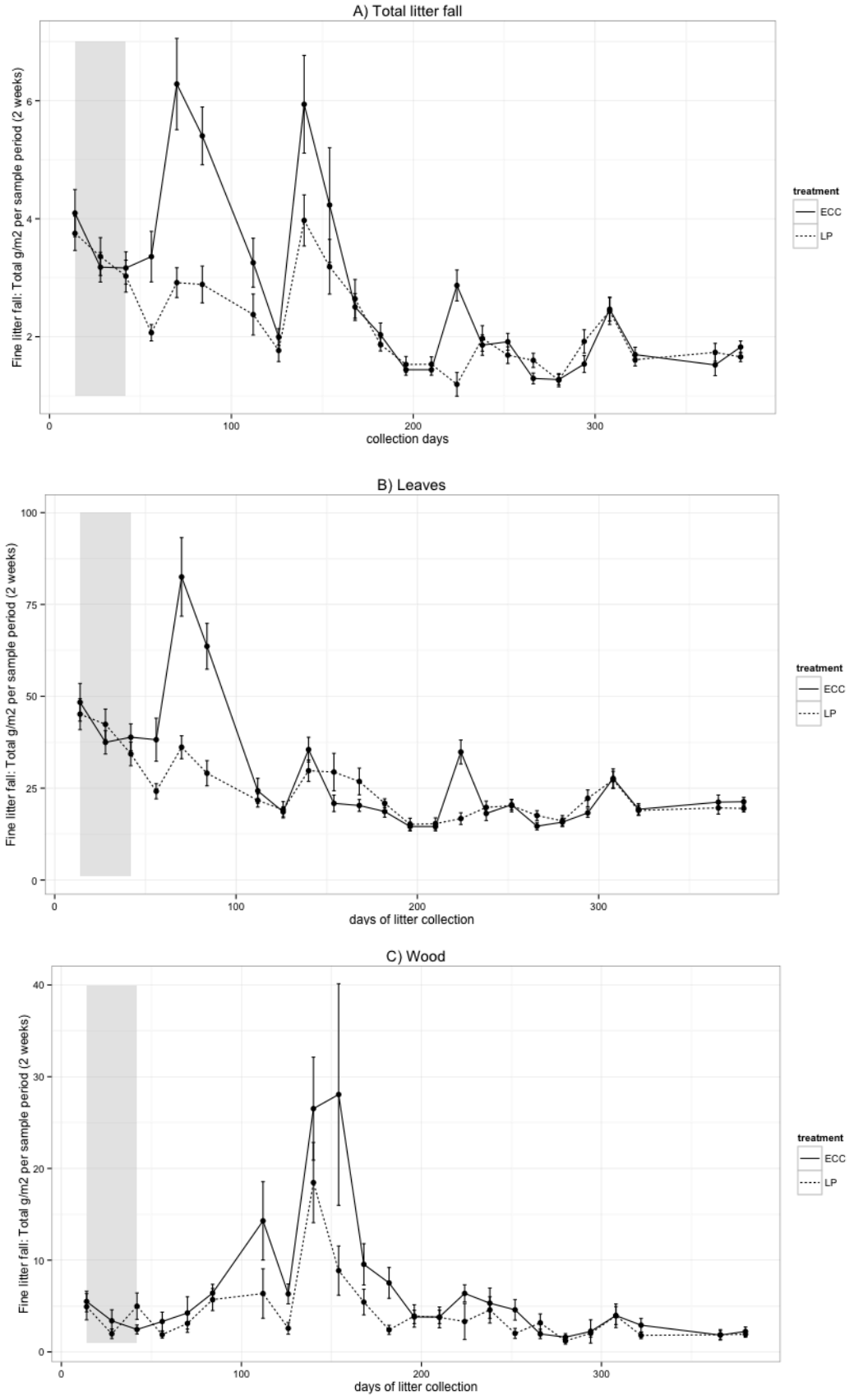

Figure 3: Mean biweekly production of fine litter ($g/m^2/day^{-1}$) for the two experimental treatments between May 2011 and June 2012. Enhanced climber cutting (n=7) and Line planting (n=7). Figure 3 (A) represents total fine litter fall; (B) leaves; (C) woody tissue. Grey shade indicates pre-treatment period.

levels between 74 - 84 days after ECC treatment was implemented (between collection day: 130 - 140). Litter fall rates after the second peak stayed constant with exception for a third peak which occurred on collection day 224.

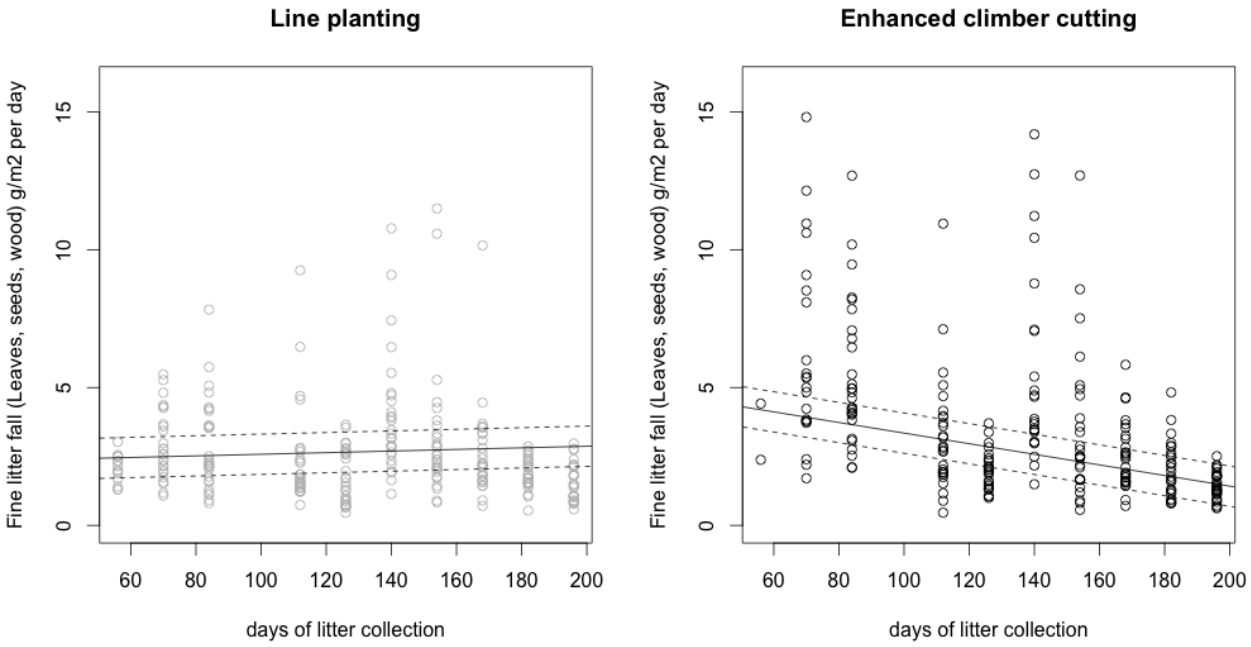

Figure 4: litter fall rates for two treatments. ECC treatment was implemented from day 56 - 70. Solid line represents difference between treatments.

LARGE LITTER PRODUCTION - Large litter fall rates remain constant between the two treatments during the entire duration of the experiment with the exception for measurement no 8 (25 November - 2 December 2011) (Appendix 2). Over the duration of the study period (June 2011 to January 2012) the ECC treatment (644.7 ± 191.2 m^3) produced 119% higher amount of large litter compared to the LP treatment (294.4 ± 191.2 m^3). However no significant difference between overall mean of litterfall between the two treatments ($F_{1,704}$= 1.08, P=0.3) was observed.

CHANGES IN CANOPY COVERAGE - ECC plots had significantly higher levels of canopy openness post-treatment compared to LP plots ($F_{1,11}$ = 5.51, P< 0.05) (Figure 5B). Pre-treatment control measurements (Figure 5A) showed no difference between ECC plots and LP plots ($F_{1,11}$ = 1.12, P > 0.05) prior to treatment. The ECC treatment increased the percentage canopy openness by 47%

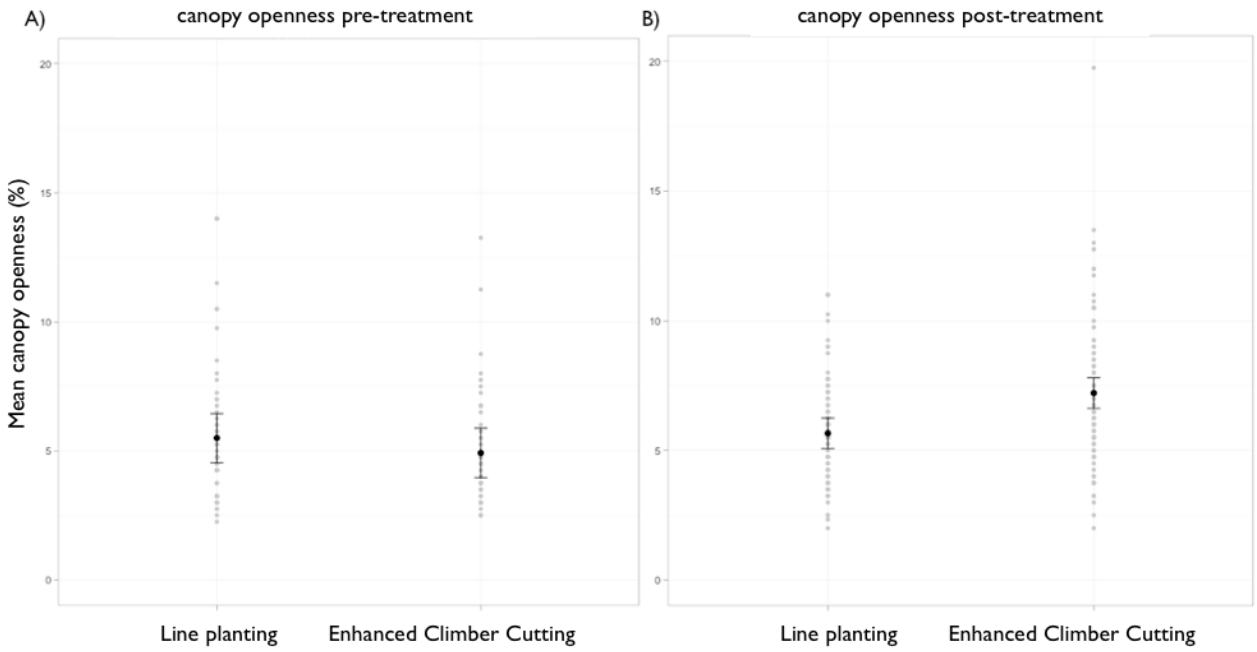

Figure 5: Difference in percentage canopy openness between ECC and LP plots at (A) pre-treatment and (B) post-treatment

Discussion

In the Malaysian state of Sabah, Malaysian - Borneo, logged over forest dominates the majority of the remaining forest cover. Understanding ecological processes such as litter fall under different tropical forest restoration strategies is crucial for the evaluation of active restoration methods that are currently being carried out in a vast scale. To date, most studies examining litterfall rates have focused on the comparison of secondary succession and primary rain forests (Ewel 1976, Ostertag et al. 2008, Saner et al. 2012) with a small amount focusing on litterfall rates under different restoration management regimes (Celentano et al. 2010). To our knowledge no publication examines litter fall dynamics in forests managed with the Enhanced climber cutting method (ECC) which has become one of the primary methods used in this region of Borneo.

DIFFERENCE BETWEEN TREATMENTS - Litter production during the entire duration of the study (1 yr.) in the ECC method was 17% higher compared to the LP method (table 2). Litter volume plays a key role on the forest floor where it affects soil nutrient status, soil water content, temperature, and pH (Sayer & Tanner 2010), all of which may have a role in changing communities of flora and fauna that inhabit the forest floor. Directly after treatment implementation, litter production increased by 130% (Figure 4). This initial increase

of litter composed primarily of leaves. This increased amount of litter (between 56 - 112 days) could provide beneficial microhabitats and support faunal litter diversity as found by Paillett et al. (2010).

A second peak in the litter fall was seen between 140 - 154 days of the experiment. This second peak was caused by larger litter — woody debris (figure 3c). After the two peaks in litter fall rates, that increased leaf and woody litter fall rates, overall litter fall rates in the climber cutting treatment returned to LP levels (control). Phillips et al. (2008), found that woody climbers can contribute to as much as 20% of leaf productivity, however in our study system, we did not find any evidence for litter fall rates being affected by the elimination of lianas and climbing plants. Overall this treatment may cause a loss in canopy arthropod diversity, which will be investigated in chapter 4.

This study highlights that the primary aim of the ECC treatment: to increase light levels for seedlings on the forest floor, was substantial (figure 4). The opening of the canopy by 47% when comparing pre and post treatment effects was seen to take place within six months after the treatment. The mean increase in light conditions from 4.9% to 7.2% full sunlight can increase growth rates of seedlings. A shade house experiment by Philipson et al. (2011), found that a small difference in light levels from 0.3% to 3.0% full sunlight, increased growth rates of 21 dipterocarp seedlings. Although no negative long-term impacts have been shown in terms of litter fall production, its primary aim to increase growth of climax species (the dipterocarpaceae family) show an overall increase in seedling growth rates without increasing mortality rates (later investigated in chapter 3). However, concerns that the increased amount of litter coupled with the increasing levels of light could also cause major changes in soil respiration rates (Saner et al. 2009) provide future avenues for research.

DIFFERENCE IN LITTER COMPOSITION - According to the general litterfall pattern, the ECC treatment primarily affected leaf litter first (figure 3b), followed by woody tissues and miscellaneous materials (figure 3c, Appendix 1e) begun to appear in later (154 days from start of experiment) as liana stems fell as they dropped from the canopy. This pattern of lianas contributing more to the forest leaf litter is parallel to studies showing that lianas invest more in leaf biomass compared to stem biomass as climbing plants do not invest

in structural support (Cai et al. 2007). The difference in the annual litter composition between the two treatments (Table 2) shows that the ECC treatment increases annual volumes of leaf, woody tissue and miscellaneous materials. However the treatment decreases the biomass of reproductive parts annually. This is likely due to the removal of lianas that often fruit regularly and outside mass fruiting cycles (Cannon, Curran & Marshall 2007b, Cannon, Curran, Marshall, et al. 2007a). Climbing plants such as lianas and bamboo contribute to tropical forests, where they are often used as host plants for a range of arthropods (Cleary et al. 2009) and as a food supply for primates (Marshall et al. 2009). An experiment carried out by Watson & Herring (2012) that removed parasitic mistletoe (which are true parasites compared to structural parasites such as lianas and other herbaceous climbers) found an overall decrease of species richness by 21%. The elimination of lianas and climbing bamboo may cause detrimental disruption to the maintenance of food supplies for fauna outside mass fruiting events (Kanamori et al. 2010, Sist et al. 2003, Paul & Yavitt 2011) and may also cause a decrease in species richness.

STABILISATION AND DYNAMICS - The short term increase in litter volume (between 56 - 112 days), caused by the treatment, could have negative side effects such as raising the amount of soil CO_2 transfer into the atmosphere (Sayer et al. 2007). Our results show that after a year of litter collection, litter production later returned to control levels suggesting that the treatment during the duration of this study does not affect the overall litter pattern. Our results contradict our hypothesis that this treatment will cause a long-term reduction of litter volume by 20%, even when lianas are known to have higher leaf turnover rates as compared to trees (Cai et al. 2009). The lack of apparent effect may be caused by the compensation of the surrounding stands of trees whereby, the increased amount of light creates an opportunity for residual stands of trees to produce new leaves. Further investigation into this is required on how this treatment will influence litter dynamics more then one year after the study.

LARGE LITTER - Although no large difference was seen between treatments, large litter was higher in forest treated with the climber cutting treatment. This may be due to the patchy distribution of large lianas that were observed to be clustered around larger trees. In order to entirely capture the effect of the ECC method on larger litter, we recommend that surveys should be carried out in entire plots rather than transects.

RECOMMENDATION FOR FOREST MANAGEMENT - Overall this study shows that the ECC treatment increases light conditions to the forest floor without changing litter fall rates after one year. To minimise the impacts of this method on residual biodiversity, we recommend that more research is done to test this treatment in a more managed manner whereby the climbers are eliminated only above desired individuals and stands of seedlings and not over entire landscapes (known as blanket climber cutting). In doing so, a remnant population of lianas can be retained in order to support faunal diversity that are reliant on fruits and flowers of lianas outside masting years. The Sabah Forestry department has also already committed to retaining large lianas that have been identified as major food sources for large birds such as the various hornbills and for primates such as Orangutans.

The timing of the treatment will also play an important role. Lianas are known to exhibit higher growth rates during the dry periods, however trees increase growth during the wetter periods (Cai et al. 2009, Schnitzer 2005). Carrying out the treatment at the transition period as the dry period ends would ensure the best growth conditions for seedlings where they would be able to maximise growth while lianas have been suppressed.

CONCLUSION - The primary aim of the ECC treatment to increase light levels on the forest floor has been shown to be successful. The increase may be beneficial for a certain amount of tree species as it imitates the natural regeneration of these forests by creating gaps. The ECC treatment also shows that it is able to improve litter quality by increasing the volume of litter added to the forest floor in the short term. However at the same time not disrupting the litter cycle as litter fall levels in the ECC and LP methods show no differences (238 days since start of experiment). In the following chapters, we will investigate the effects of our treatment for seedlings grown within a forest matrix testing if this treatment increases growth rates of studied seedlings without compromising mortality. We will also investigate if this treatment causes detrimental changes in above ground biodiversity that will be investigated in chapter three and four respectively.

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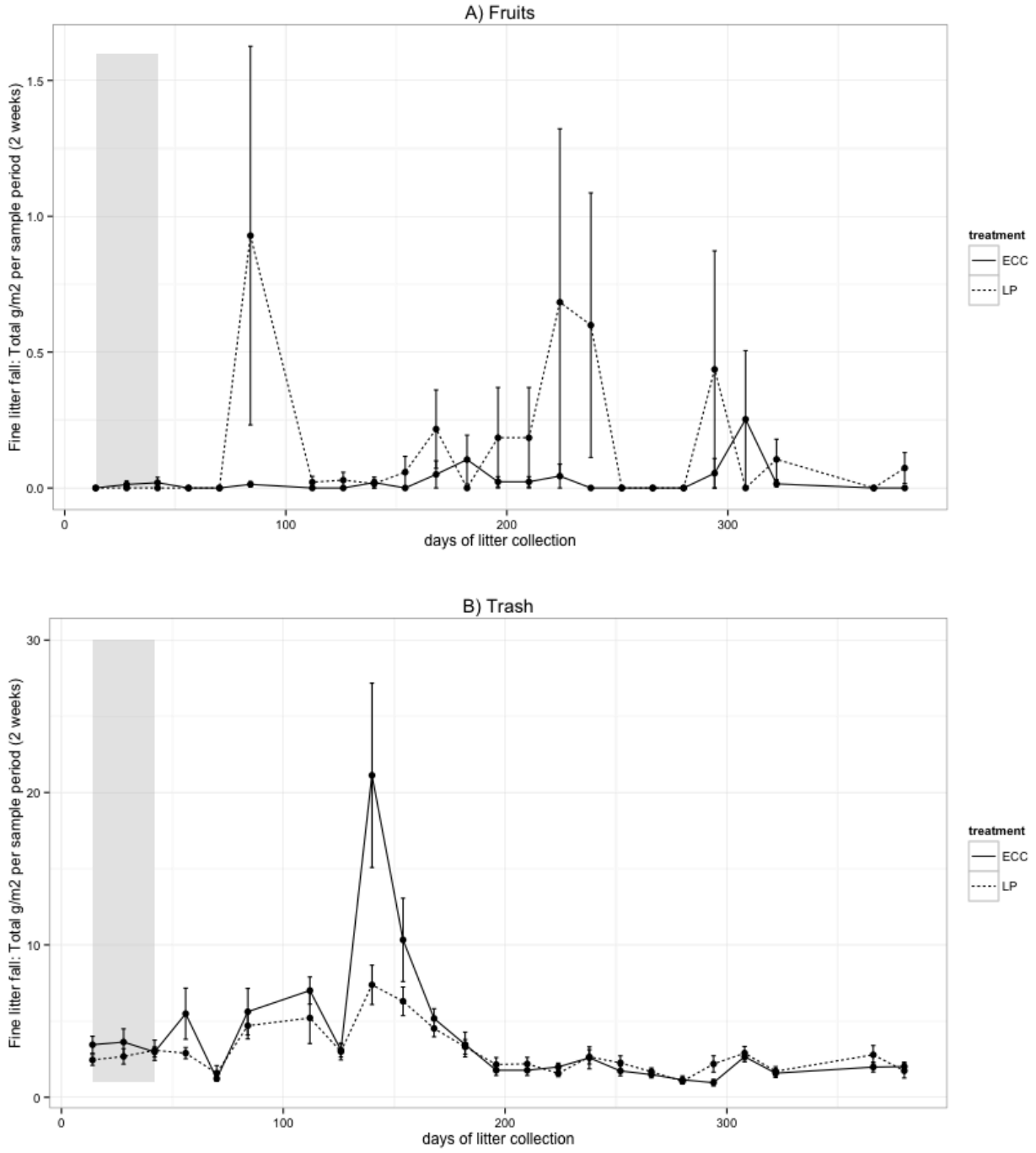
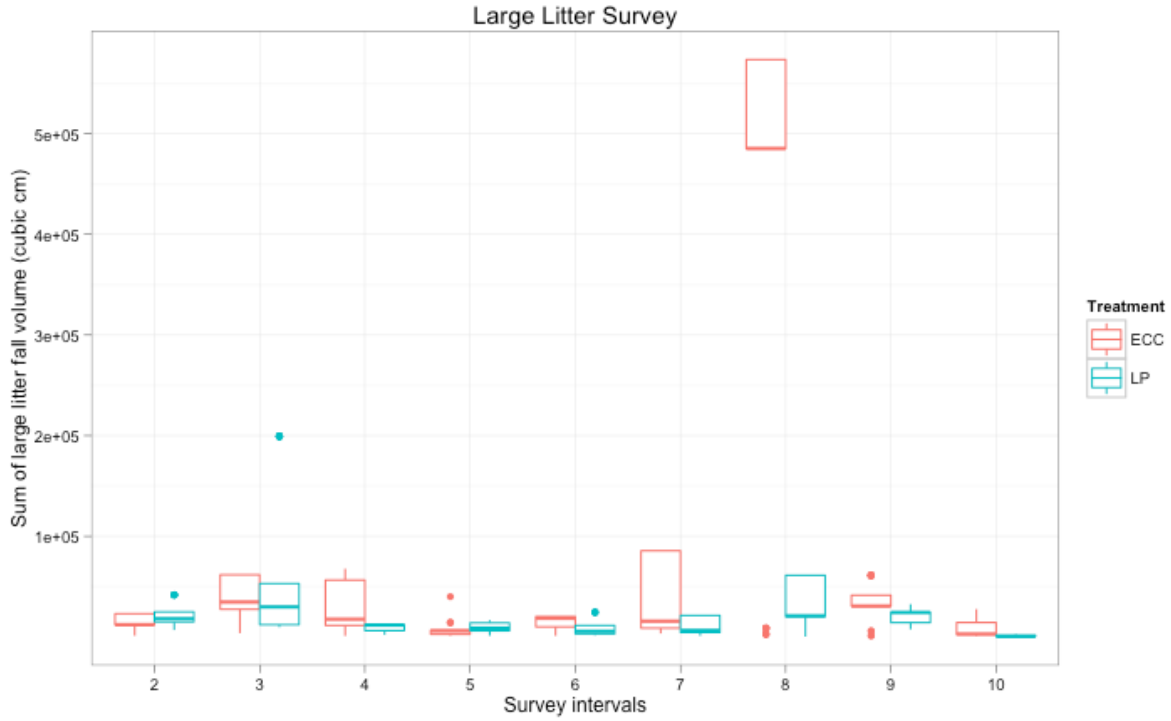
Appendix



Appendix 1: Mean biweekly production of fine litter ($g/m^2/day^{-1}$) for the two experimental treatments between May 2011 and June 2012. Lines represents trends of litter fall rates using a generalised additive model as a smoother. Enhanced climber cutting (n=7) and Line planting (n=7). Appendix 1;(A) Fruits and B) represents miscellaneous materials. Gray shade indicates pre-treatment period.



Appendix 2: Large litter fall rates for the two treatments. Enhanced climber cutting (ECC) shown in orange and Line planting (LP) shown in green.

Chapter 3: **Effects of two major forest restoration regimes on the growth and survival of seedlings of 16 Dipterocarp species**

Effects of two major forest restoration regimes on the growth and survival of seedlings of 16 Dipterocarp species

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Abstract

Logged lowland tropical forests of South-east Asia are currently being restored to regenerate its values in terms of its future logging capacity, ability to sequester and store carbon and to enhance its capabilities of retaining biodiversity. Methods used to regenerate these forests vary depending on the level of degradation. The reduction of climbing plants (the climber-cutting silvicultural method) has been widely used as a cheap method with the main intention for increasing light levels to naturally occurring or enrichment planted seedlings on the forest floor. However, how effective the enhanced climber-cutting method is in increasing growth is not known. Moreover, such silvicultural methods may cause unintended shifts to seeding composition as light levels are increased, favoring seedlings which can utilise this newly created condition. In this study we compare the growth and survival of seedlings grown under conventional line planting methods with those grown under enhanced levels. Out of 16 enrichment planted species, nine species showed significant increases in growth rates in the enhanced climber-cutting treatment, with a further seven showing non-significant difference. On average the climber-cutting method increased seedling basal diameter growth rates (compared at a common size: SGR) by 28%, with the largest difference in SGR seen in *Shorea beccariana,* showing an 88% increase in growth rates under enhanced climber-cutting methods compared with standard line planting methods. *Parashorea malaanonan* responded the least out of the 16 studies species and grew 14% more in the line planting treatment compared to the climber-cutting treatment. We found the enhanced climber-cutting treatment to increase aboveground biomass of planted seedlings by 56% then the line planting method. Our findings show no negative results in terms of seedling mortality rates amongst our studied species, therefore suggesting that this method may not put species in a competitive disadvantage.

Introduction

Over the last few decades, tropical forest have been threaten by over exploitation for the timber they contain (Curran et al. 2004). As the economically valuable timber is diminished, these lands often become targets for conversion for agricultural purposes (Sodhi et al. 2004, Koh & Wilcove 2008). Throughout Southeast Asia, roughly 63% of the total remaining forest is dominated by logged and degraded forests (Kettle 2010). Selective logging is used as the primary method of timber extraction which causes disturbance, and damages up to 50% of trees across all size classes (Johns 1988). However despite these damages, these forest are still capable of retaining a large percentage of its original biodiversity and remain to provide ecosystem services such as watershed protection, sustaining biodiversity and carbon sequestration and storage (Lewis 2009, Edwards et al. 2011, Berry et al. 2010).

The dynamics of how logged forest regenerate after large disturbance has been well documented in different natural regeneration stages (Bischoff et al. 2005, Sist & Nguyen-The 2002) and with different management strategies (Ohlson-Kiehn et al. 2006). The intensity of post logging management varies with the level of degradation, the desired final output (Chazdon 2008). In forests where seedling stocks have been extensively damaged, reintroduction by enrichment planting has been used (Moura-Costa et al. 1994, Chan et al. 2008, Chai 2006). However if residual seedling stocks still persist, silvicultural methods to reduce above ground competition such as liberation thinning of pioneer trees and cutting of climbing plants are often used (Paul & Yavitt 2011, Gerwing 2001). Methods used also vary according to project budgets as some methods require more resources then others (Pérez-Salicrup et al. 2001, Ohlson-Kiehn et al. 2006). In the Malaysian state of Sabah, on the island of Borneo, vast areas have been treated with either enrichment planting or by silvicultral treatments. Conventional enrichment planting involves planting desired tree species along planting transects which are often cleared manually by removing competing vegetation on the forest floor (Chai 2006). This method however can be enhanced by treating entire rehabilitated plots by silvicultral treatments such as climber-cutting (Gerwing 2001). The climber cutting treatment is also often prescribed to forest stands that have large enough stocks of desired species and can be applied without the need for enrichment planting, this standalone treatment is often termed liberation thinning. Sabah Forestry Department's annual reports,

reported up to 17,490 hectares (from 2007 - 2011) have been restored using enrichment planting and 130, 351 hectares (from 2006 to 2011) have been treated with the climber-cutting method.

With cheap application costs and with positive outcomes, the stand alone climber-cutting silvicultral method has been projected to be used in a more extensive scale. Woody climbers (lianas) and herbaceous climbing vines are often seen to increase and dominate areas that have been extensively disturbed by natural processes (Paul & Yavitt 2011), and by human induced disturbance such as logging (Pinard & Putz 1994). In recent times, dominance of lianas and climbing plants have been increasing due to elevated concentrations of atmospheric carbon (Phillips et al. 2002, Granados & Körner 2002). Large scale land management organizations in the state of Sabah; Sabah Forestry Department and the Sabah Foundation have both committed to continue the use of this silvicultral method (Y Sau Wai 2012, pers. comm.). The primary aim of the climber-cutting silvicultral treatment is aimed at increasing available light conditions to seedlings on the forest floor. Early results of this method show that the climber-cutting method is capable of increasing canopy openness levels by 47% (see chapter two) and may have consequences to future species composition of managed forests.

For seedlings on the forest floor, amount of light levels is often considered one of the most significant limiting resources in tropical forests (Whitmore et al. 1993, Grubb & Burslem 1998). A large amount of work has investigated the role of light and how it is responsible for partitioning different forest species based on growth performance (Brown & Whitmore 1992, Whitmore & Brown 1996). The ability of tropical trees to maintain high levels of species diversity has often been attributed to the ability of seedlings to partition themselves by having different growth and mortality levels in a closed canopy forest (Grubb 1977, Pacala et al. 1996, Wright 2002). The trade off between high growth rates in high light and survival in shaded conditions is maintained by the differences among seedlings and the variation in light availability. Species are often characterized into two continuous categories, light-demanding species that quickly colonise forest gaps and exhibit high growth rates if light levels remains high however, die quickly in shaded environments. Shade-tolerant species that are often limited by slow growth have the capabilities to withstand longer periods of being shaded. All dipterocarps are considered shade tolerant however they often show a variation to the

levels that they tolerate. There is a large amount of research that attempts to disentangle and explain these differences among species by examining species functional traits which is defined as: measurable properties of an organism that is strongly influence/coordinated with an individuals performance.

In this study, we test the effects of two of the common forests restoration strategies carried out in the Malaysian state of Sabah. We investigate the growth and mortality performance of 16 predominately shade tolerant dipterocarp species over a four year period in a large scale field experiment. The following hypothesis was tested: (1) Does the enhanced climber-cutting method increase growth rates of enrichment planted seedlings more then the standard line planting method by increasing light availability; (2) does the increase in light levels affect mortality; and (3) does the species studied differ in growth rates and mortality responses.

Methods

STUDY SITE - This study was conducted from September 2009 to September 2013 in a large scale forest restoration experiment: The Sabah Biodiversity Experiment (SBE) (05°05'20" N, 117° 38'32" E) for a full description of the site refer to Hector et al. (2011). The Sabah Biodiversity Experiment is located 65 kilometers along the main logging road from the Danum Valley Field Centre (4°58'49" N, 117°51'19" E) in the Malaysian state of Sabah, Borneo (Figure 1). The SBE consists of 500 ha of logged lowland mixed dipterocarp forest that is currently being rehabilitated. The Malua forest reserve that sits within the Yayasan Sabah forest concession (1 million ha) was selectively logged during the early 1980's. The surrounding reserve was then consecutively re-logged in 2007 with the exclusion of the study site. Pre-logging volume of trees was estimated at 193 - 221 m^3 ha^{-1}, from the total, 180 - 216 m^3 ha^{-1} composed of trees belonging to the dipterocarp family (Hector et al. 2011). Annual precipitation recorded at the field station averaged 3000 mm / year, with an average temperature of 25.5°C. Soil in the region is characterized as orthic acrisol (pH < 6) with a base saturation of 81% (Hector et al. 2011).

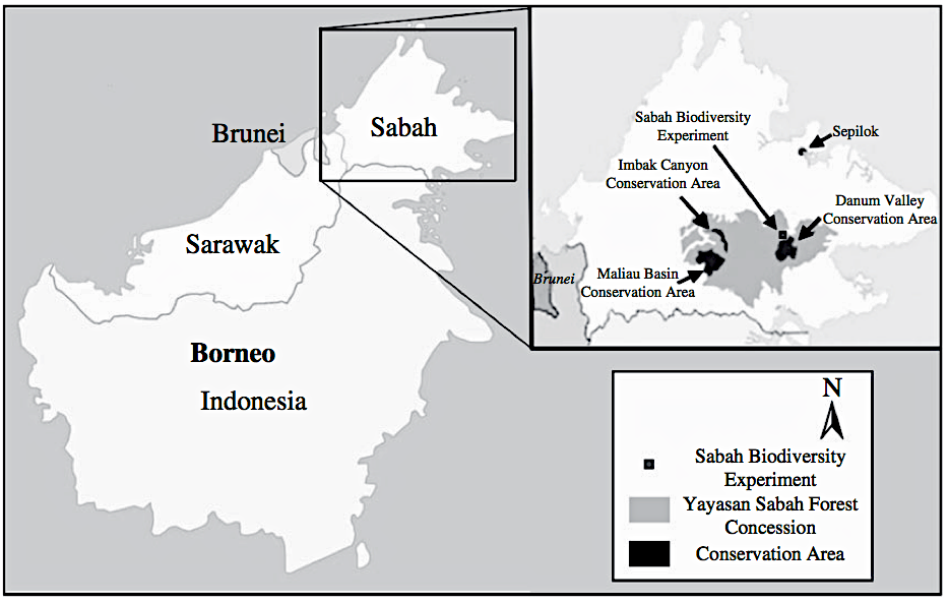

FIGURE 1: Location of study site in the Malaysian state of Sabah, Borneo (Hector et al. 2011).

EXPERIMENTAL DESIGN - Experimental plots were divided into three main treatments: (1) standard line planting (LP), (2) Standard line planting with enhanced climber-cutting (ECC) and unplanted and un-manipulated control plots (Figure 2a). Standard line planting plots consist of 200 m long transects with 3 m wide strips. Understory herbaceous plants were cleared manually from the 3 m wide strips. Parallel 200 m

long planting transects run in a north to south direction 10 m apart (Figure 2b). Planting constrains were adapted from the standard rehabilitation methods widely used in Malaysia (Chan et al. 2008, Ådjers et al. 1995).

Enhanced climber-cutting plots consisted of standard line planting methods with an additional treatment in which all climbers (lianas and climbing bamboo (*Dinochola* spp)) >1 cm diameter were manually eradicated by machete/parang. The enhanced climber-cutting treatment was implemented from 8 July 2011 - 23 July 2011. Line planting and enhanced climber-cutting experimental plots were planted in 2003 and seedlings lost by mortality were replanted in 2008. In both line planting and enhanced climber-cutting plots, we randomly selected two planting lines to be monitored as part of this experiment . Control plots consisted of plots without any silvicultral treatments carried out within them, where two rows (200 m) of seedlings were planted (north to south direction) (Figure 2b). Seedlings here were also separated 3 m apart along the lines and were planted the logged forest matrix, no three meter planting strips were cleared. Seedlings of both the line planting plots and the enhanced climber-cutting plots were one year old at the first census period. Seedlings of the control plots however, was <1 month at first census.

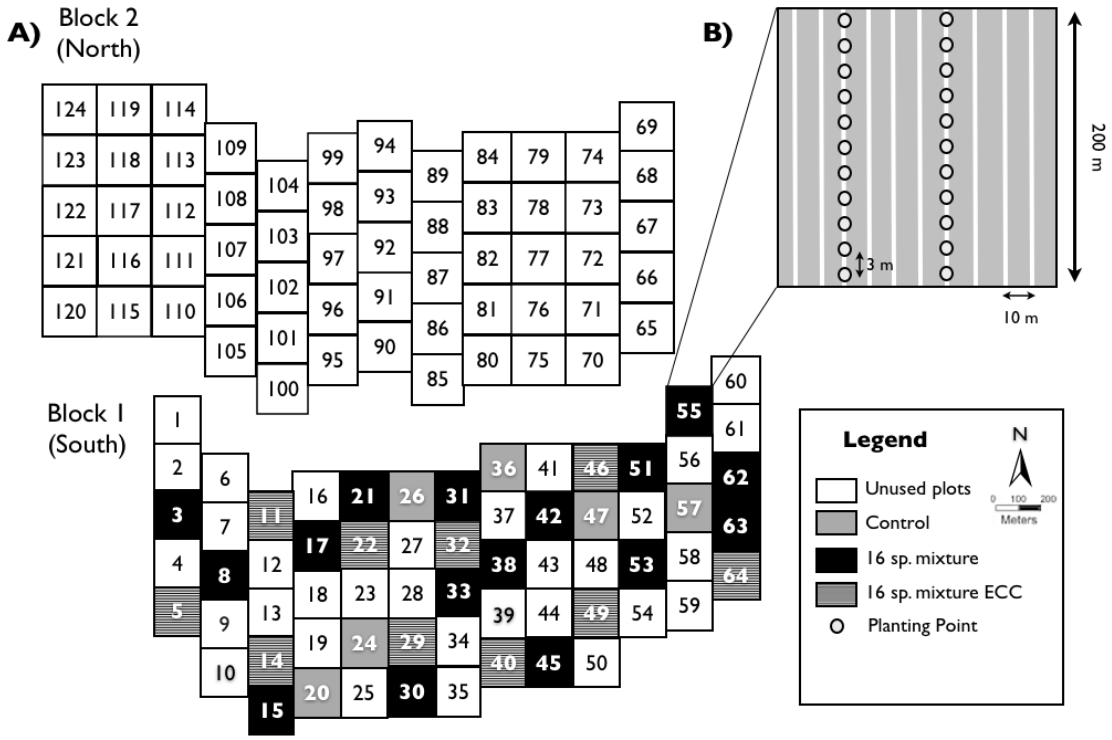

FIGURE 2: (A) selection of plots within the SBE. Grey shaded plots represent control plots (n=6), Black plots represents line planting plots (n=16) and striped plots represent enhanced climber-cutting plots (n=10). (B) Seedlings planted 3 m apart along parallel planting lines 200 m long separated 10 m apart.

STUDY SPECIES - Sixteen species of trees belonging to the family of Dipterocarpaceae were used in this experiment. Species included ten from the genus *Shorea*, two from *Parashorea* and *Hopea*, and one from *Dryobalanops* and *Dipterocarpus*. Dipterocarps dominate the canopy and are often targeted as trees logged for their high timber value (Burgess 1966). The selection of species was based on seedling availability during the set up of the experiment (2002) and natural occurrence of the species in adjacent unlogged forests. Table 1 lists the species used, species authority and their conservation status according to the IUCN Red List.

TABLE 1: List of Dipterocarp species planted

Genus	Species	Abbreviation	Species authority	IUCN Status
Shorea	*johorensis*	SJ	Foxw.	Critically endangered
	gibbosa	SG	Brandis.	Critically endangered
	argentifolia	SA	Sym.	Endangered
	faguetiana	SFG	Heim.	Endangered
	leprosula	SL	Miq.	Endangered
	macrophylla	SM1	Ashton	Vulnerable
	macroptera	SM2	King	-
	ovalis	SO	Korth.	-
	parvifolia	SP	Dyer.	-
	beccariana	SB	Bruck	Not listed
Parashorea	*malaanonan*	PM	(Blanco) Merr.	Critically endangered
	tomentella	PT	Meijer	Not listed
Hopea	*sangal*	HS	Korth.	Critically endangered
	ferruginea	HF	Parijs	Critically endangered
Dryobalanops	*lanceolata*	DL	Burck	Endangered
Dipterocarpus	*conformis*	DC	Slooten	-

SEEDLING VARIABLES - Seedlings were measured at six time intervals from September 2009 to September 2013. Seedling height to apical meristem was measured from plant base. Plant base was taken at the highest uphill point when a plant occurred on a slope. Basal diameter growth was measured 2 cm from the base of the plant. When roots or buttresses were encountered the basal diameter was taken directly above the formations. Diameter at breast height (DBH) was measured for plants that were higher than 1.3 m. Plants would only be considered as dead when base of stems are found to be no longer green when exposed.

Seedlings were remeasured when an unusual value (e.g: extreme shrinkage) occurred during field measurements and changes were added to the database with updated dates of measurement.

CANOPY AND FOREST VARIABLES - Canopy coverage above each seedling was estimated with a spherical densiometer (Lemmon 1956) at every census/measurement interval for the duration of the experiment. Canopy height survey was estimated with the use of a clinometer (Suunto PM-5/360 PC) at six points intervals (50, 100 and 150 m) along) along studied planting lines. Basal area was estimated at six 50 m intervals using the variable - radius plot (point sampling) method ((Avery 1975, Bitterlich 1984)). Prism sweeps were carried out using prisms with a 10 m^2 ha^{-1}. Distance from sample point and diameter at breast height (DBH) of all borderline trees were measured.

SPECIES TRAITS - Functional trait data was accumulated from experiments conducted at the experimental site (Philipson 2009, Philipson et al. 2012). Leaf area was calculated by photographing all leaves (n= 3285 plants) using the imageJ software (Abràmoff, Magalhães & Ram 2004). Specific leave area (SLA) was calculated using dried leaf mass (dried at 60°C to constant mass). Leaves were dried and grounded to extract nitrogen using the Kjeldahl method (Lowther 1980) and organic carbon using the Walkley-black method (Walkley & Black 1934). Wood density estimates were measured using the lower 30 m of sapling stems grown in shade house experiments described in Philipson (2012). Methods used to calculate wood densities are described by Chave (Chave et al. 2005). Seed size data was collected during a masting event in 2010 for experiments carried out by O'Brien (2013). Seed size was averaged over 1887 (n= 49 - 137 seeds per species) collected seeds that were oven dried and weighted individually.

BIOMASS ACCUMULATION - For the calculation of aboveground biomass (AGB), we obtained a generic dipterocarp seedling specific gravity for the range of species from O'Brien (2013) and applied an allometric equation developed on seedlings in this study (See eqn.1). Where AGB is the estimated above ground biomass (in g per tree, including stem branch and leaf biomass), diameter: the seedling basal diameter, height: seedling height to apical meristem (in cm).

AGB=*Exp(LogAGB = -4.499274+1.449707*log(diameter)+1.0146*log(height))*

[eqn. 1]

DATA ANALYSIS - Analysis was carried out using the software package R (version 2.15.0: R Core Development Team 2012). Species growth rates between different restoration strategies were analyzed using linear mixed effects models using the 'nlme' package version 3.1-105 (Pinheiro et al. 2008). We calculated size-specific relative growth rates (SGR) in order to take into account that seedling exhibit differences in growth rates depending on seedling start size (Turnbull et al. 2008, Philipson et al. 2011). Seedlings size was standardize by extracting parameters from the fitted growth model and calculating SGR as shown below in eqn 2, where M_c is a common reference size, Species shared a single value of the scaling exponent β within each analysis. Differences in diameter SGR and light among studied species are caused by the differences in the growth coefficient. finally α and relative ranking are not dependent on reference size. In the growth analysis, measurement interval (day), treatment and species was considered as fixed factors. Both seedling number and line were nested within plot. The best model was selected using a stepwise procedure retaining model terms based on Akaike's Information Criterion (AIC).

$$SGR = \alpha M_c^{(\beta - 1)}$$

[eqn. 2]

Mortality rates were analysed using the 'lme4' package version 0.999999-0 (Bates 2008). We modelled the probability of mortality at standardised size (as carried out in the growth model) and took species and light conditions as fixed factors. Measurement intervals and seedling identity were used as random factors. A binomial error distribution with a complimentary log- log link was used to analyse seedling mortality.

Results

A total of 2107 dipterocarp seedlings were planted into a logged forests and were measured over a 2.6 year period (953 days) and at six time intervals. Seedlings showed constant growth rates between both treatments prior to the climber-cutting implementation (0-400 days) (Figure 3, shaded).

SEEDLING GROWTH - Overall there was substantial variation in basal diameter SGR out of the 16 studied dipterocarp seedlings. All species increased in growth rates in the climber-cutting treatment with the exception of one species (*Parashorea malaanonan)* that showed a weak signal of having higher growth rates in the line planting method. Nine species exhibited a large difference in growth rates between the two treatments (Figure 4). The remaining seven species showed marginal to no difference in growth rates in different management treatments.

Figure four shows seedings ranked in order of difference from largest in basal diameter SGR rates among treatments (left) to lowest (right). Within the line planting method, seedlings showed a variation in growth rates where the fastest growing species (*Shorea parvifolia*) grew 68% faster compared to the slowest growing species (*Dipterocarpus conformis*) with respectively; 0.0013 compared to 0.00075 mm mm^{-1} day^{-1}. In the enhanced climber-cutting method growth rate variation increased, the fastest growing species (*Hopea ferruginea*) grew 85% faster compared to the slowest growing species (*Shorea ovalis*), with a variation from respectively; 0.0017 compared to 0.00094 mm mm^{-1} day^{-1}.

The climber-cutting method increased overall seedling basal diameter SGR by 28%, with the largest difference in SGR seen in *Shorea beccariana,* showing an 88% difference in growth rates when comparing the enhanced climber-cutting method against the line planting method. *Parashorea malaanonan* responded the lowest out of the 16 studied species and grew 13.77% higher in the line planting treatment compared to the climber-cutting treatment, this result however was statistically weak.

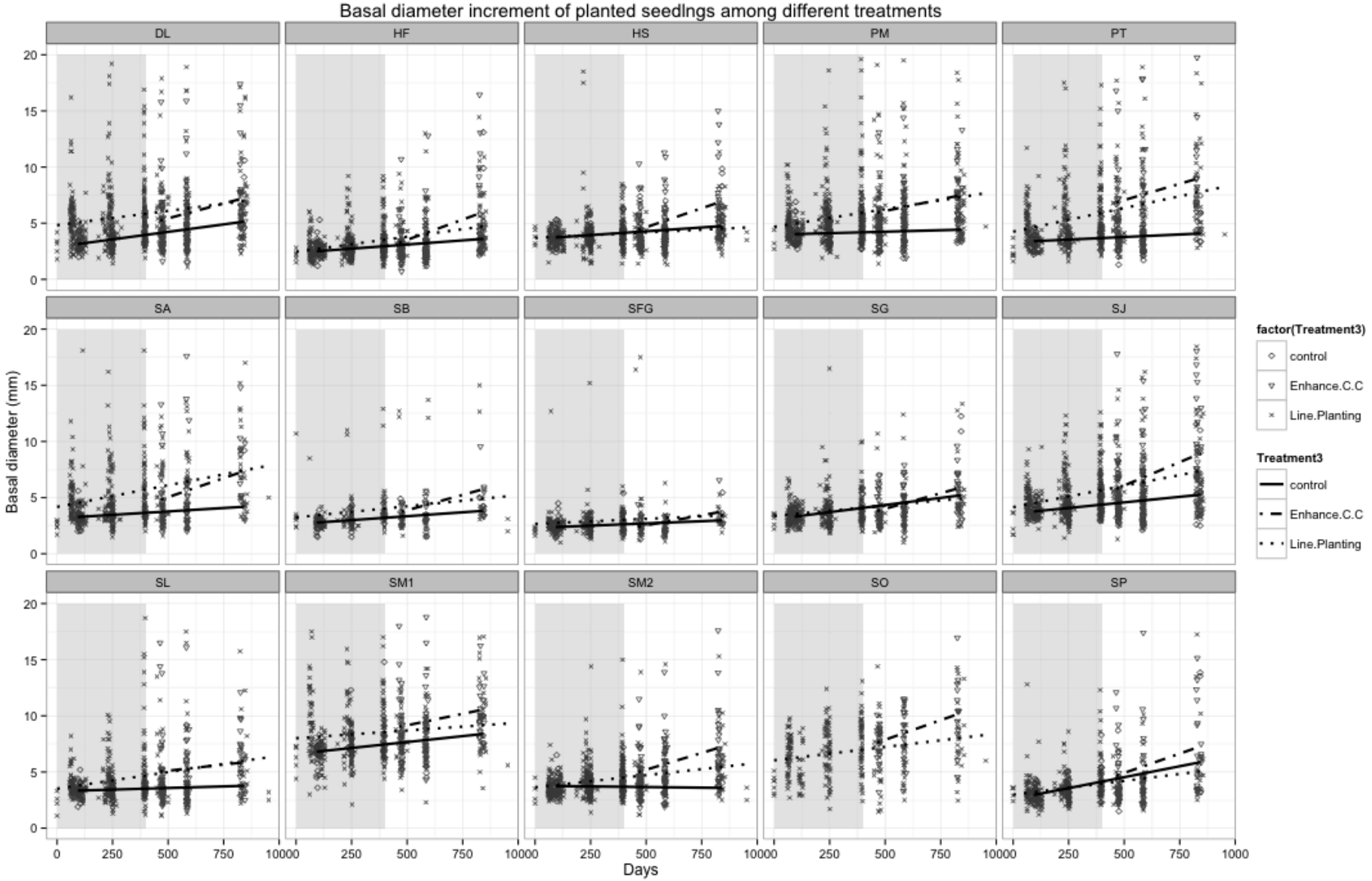

FIGURE 3: Basal diameter (BD) increment of studied species prior and post climber-cutting treatment. Shaded grey area represents pre-climber-cutting period. Solid and dashed lines represents linear model.

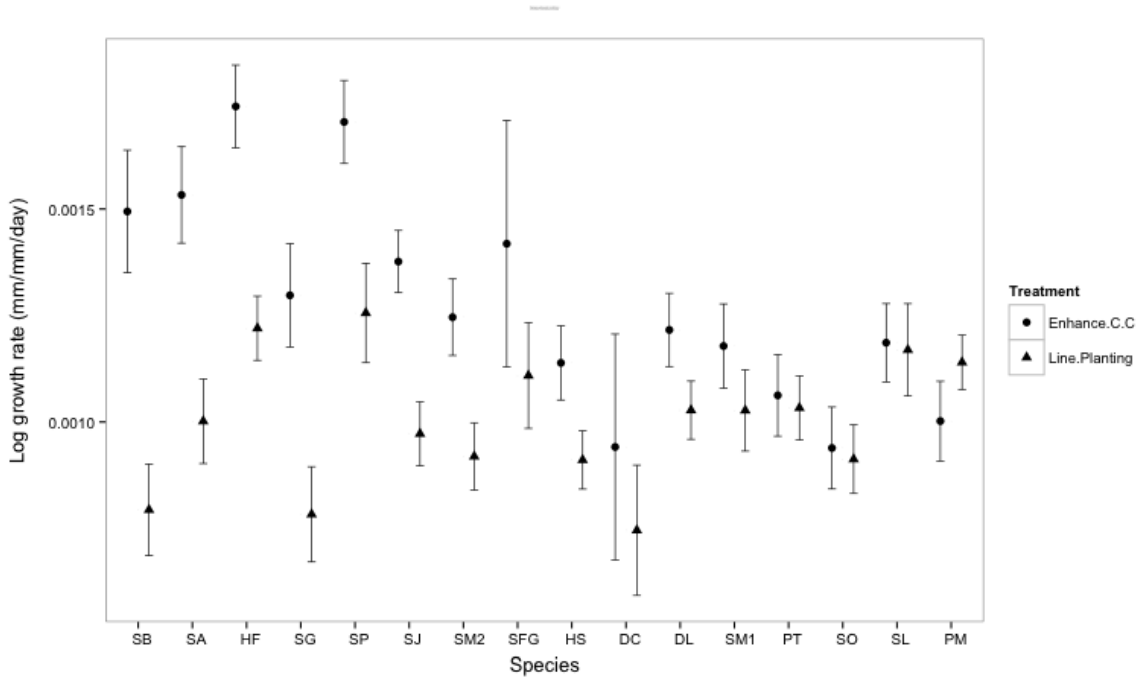

FIGURE 4: SGR Basal diameter growth rates of 16 dipterocarp seedlings in experiment. Solid circles represent seedlings grown in enhanced climber-cutting treatment. Solid triangle represent seedlings grown in line planting plots. Species ordered from highest response rate (left) to lowest (right).

We found that both fastest growing species in the line planting method (*Hopea ferruginea* and *Shorea parvifolia*), retained the fastest growing ranks (1 and 2) in the climber-cutting method (Table 2). The slowest growing species in the line planting method (*Dipterocarpus conformis*), retained one the slowest growing in the climber-cutting method where it was ranked the slowest in the line planting method and ranked second slowest growing in the enhanced climber-cutting method. Table 2 shows species rank order of species SGR in the two experimental treatments. Our results show that there are a high amounts of crossovers in species ranking between intermediate ranked seedlings (table 2) with highest ranking shifts being for for *Shorea beccariana* and *Parashorea malaanonan* where both showed the largest shift of 10 places. *Shorea beccariana* was among the slowest growing species in the line planting method (ranked 14), however increased in ranks to one of the faster growing species in the enhanced climber-cutting method (ranked 4) (table 2).

TABLE 2: Species rank order of basal diameter SGR ± SE (mm mm^{-1} day^{-1}) in experimental treatments from: fastest growing (1) to slowest growing (16) including the species shifts in ranks among treatments.

Genus	Species	SGR in conventional line planting (± SE)	Rank in conventional line planting	SGR in enhanced climber-cutting (± SE)	Rank in enhanced climber-cutting	Rank shift
Shorea	*johorensis*	0.00097 ± 0.00008	10	0.00138 ± 0.00007	6	+4
	gibbosa	0.00078 ± 0.00011	15	0.00130 ± 0.00012	7	+8
	argentifolia	0.00100 ± 0.00010	9	0.00153 ± 0.00011	3	+6
	faguetiana	0.00111 ± 0.00012	5	0.00142 ± 0.00029	5	0
	leprosula	0.00117 ± 0.00011	3	0.00119 ± 0.00009	10	-7
	macrophylla	0.00103 ± 0.00010	8	0.00118 ± 0.00010	11	-3
	macroptera	0.00092 ± 0.00008	11	0.00125 ± 0.00009	8	+3
	ovalis	0.00091 ± 0.00008	12	0.00094 ± 0.00010	16	-4
	parvifolia	0.00126 ± 0.00012	1	0.00170 ± 0.00010	2	-1
	beccariana	0.00079 ± 0.00011	14	0.00149 ± 0.00014	4	+10
Parashorea	*malaanonan*	0.00114 ± 0.00006	4	0.00100 ± 0.00009	14	-10
	tomentella	0.00103 ± 0.00008	6	0.00106 ± 0.00010	13	-7
Hopea	*sangal*	0.00091 ± 0.00007	13	0.00114 ± 0.00009	12	+1
	ferruginea	0.00122 ± 0.00008	2	0.00174 ± 0.00010	1	+1
Dryobalanops	*lanceolata*	0.00103 ± 0.00007	7	0.00122 ± 0.00009	9	-2
Dipterocarpus	*conformis*	0.00075 ± 0.00015	16	0.00094 ± 0.00027	15	+1

SEEDLING MORTALITY - Species showed an intrinsic difference of mortality that remained constant over the duration of the study period. Difference however was weak (figure 5) between both experimental treatments. We found that the probability of mortality to decrease with an increase in canopy openness. Eight of the studied species showed higher mortality rates in the enhanced climber-cutting treatment as compared to the line planting treatment. This is shown in figure 5, where a difference in intercepts in their probability of mortality was found. These included: *Dryobalanops lanceolata*, *Hopea sangal*, *Parashorea malaanonan*, *Parashorea tomentella*, *Shorea faguetiana*, *Shorea johorensis*, *Shorea ovalis* and *Shorea parvifolia*. Our results overall show that there are minimal difference in seedling probability of mortality response to the two treatments.

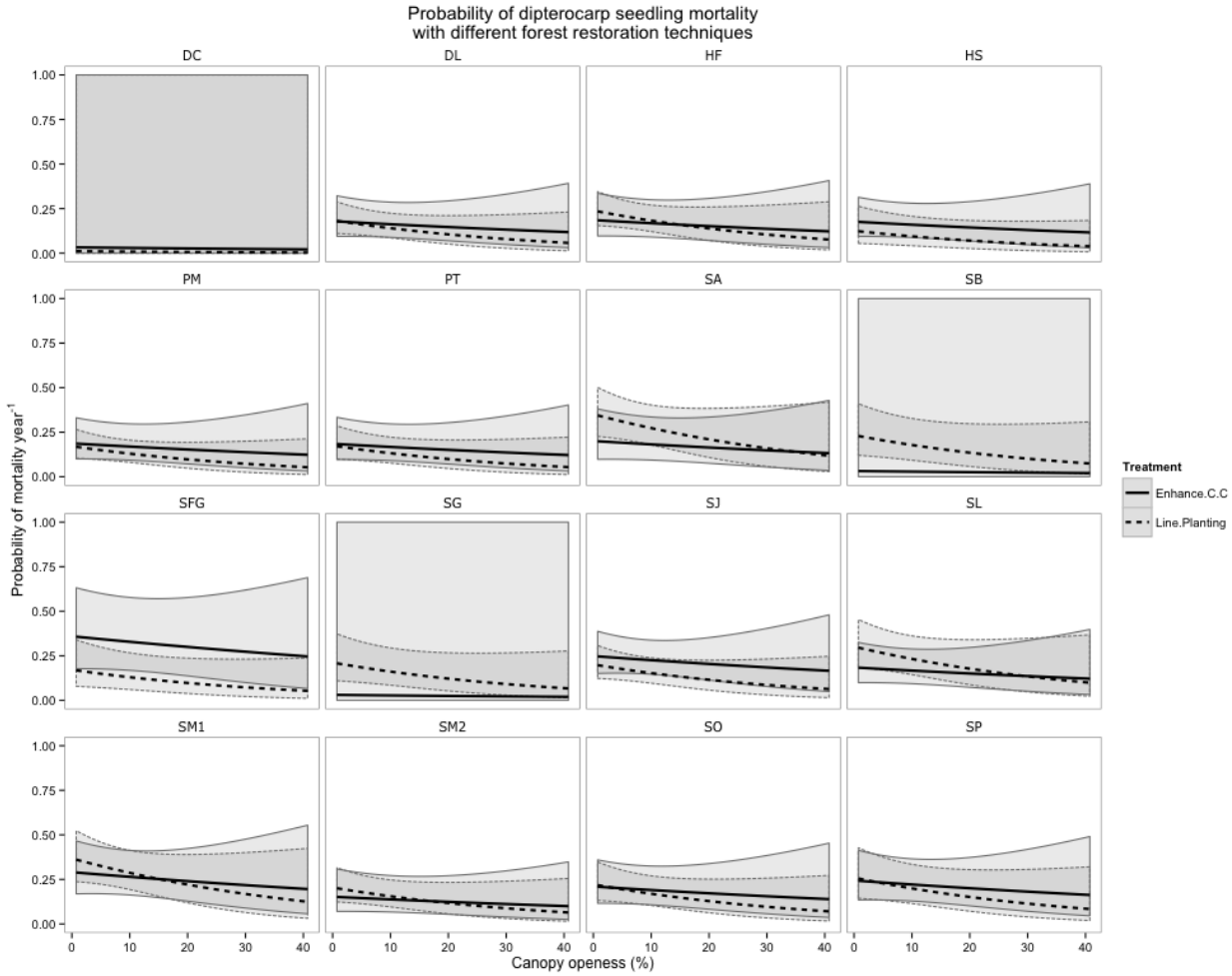

FIGURE 5: Mortality of 16 enrichment planted seedlings in both forest management treatments along a natural canopy openness gradient within plots. Panels depicts each species, where lines represent expectations from model fitted to the data. Solid black lines represent the enhanced climber-cutting treatment and dashed line represents line planting treatment. Shaded grey area represents standard error of the fitted model.

GROWTH AND MORTALITY TRADEOFF - We correlated the mean SGR and mean mortality for 16 of the studied species. We found a weak performance rank shift can be seen among the two management techniques. In the standard line planting method, growth rates was inversely related to mortality (Pearson's Cor: -0.20). Seedlings that exhibited high growth rates, exhibited low mortality rates (Figure 6 top). However in the climber-cutting treatment, growth rates were seen to have a positive relationship with mortality (Pearson's Cor: 0.17) (Figure 6 bottom).

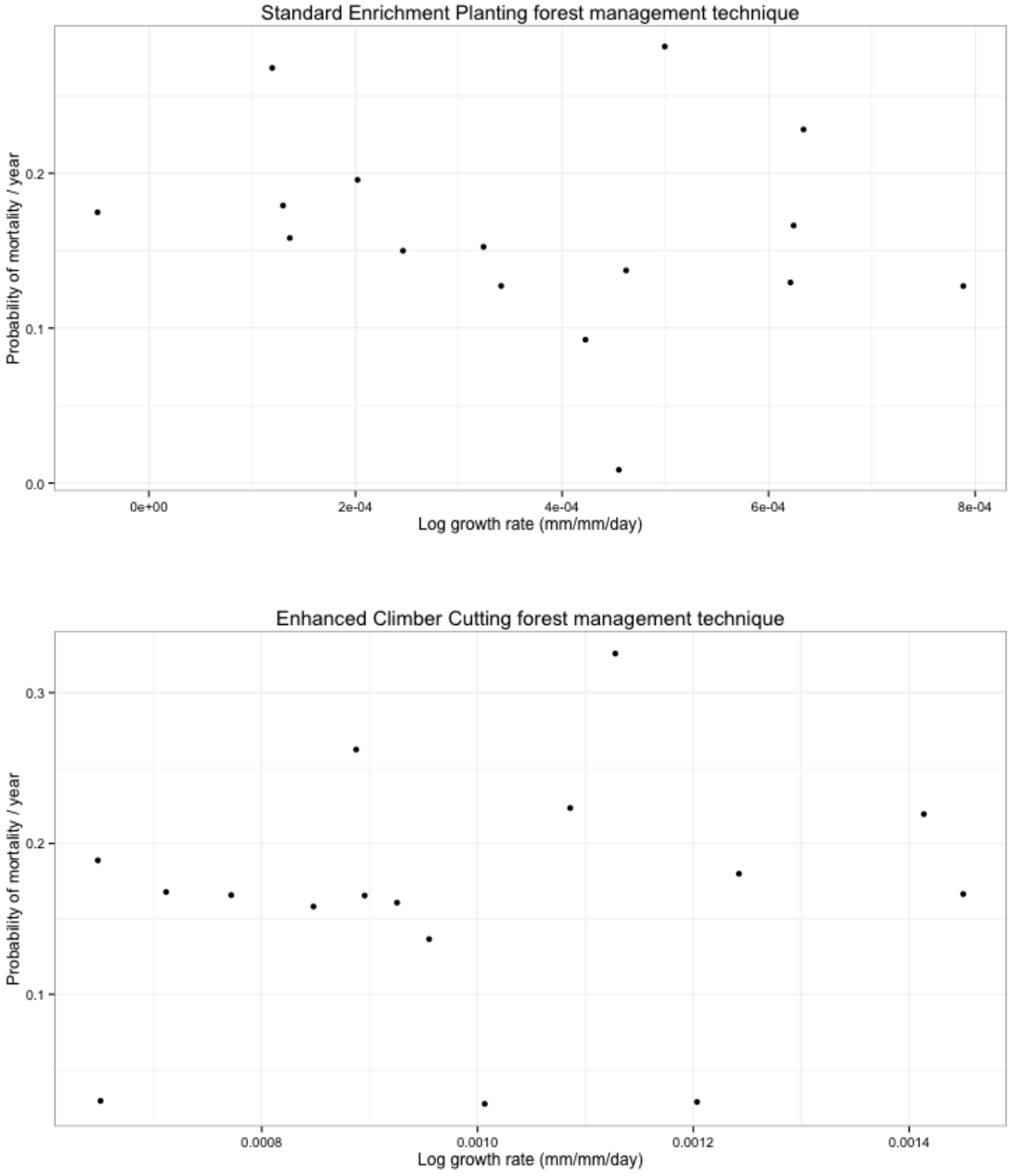

Figure 6: Tradeoff between probability of mortality and growth rate of seedling in (above) standard line planting (Pearson's Cor: -0.20) and in (bottom) enhanced climber cutting (Pearson's Cor: 0.17). Annual mortality rate and growth rate taken from average canopy openness light conditions for both treatments.

TABLE 3: Above ground biomass (kg ha^{-1}, $individual^{-1}$) (AGB ± SE) increment for planted seedlings in line planting (n=16) and enhanced climber-cutting (n=10) plots. Enhanced climber-cutting treatment is applied after third measurement interval.

Treatment	Measurement interval (average days)	N	AGB (kg) ± SE	Percentage AGB (kg) increase (Pre treatment: measurement 1-3, Post treatment: measurement 4-6)	Overall AGB (kg) Percentage increase (Measuremen time 1 - 6)	% mortality
Line planting	1 (0)	974	5.98 ± 1.05			
	2 (149)	775	6.34 ± 1.40	36.0%		
	3 (302)	665	8.13 ± 1.92			
	4 (379)	618	7.21 ± 1.37		132.8%	48.9%
	5 (497)	593	10.39 ± 2.94	93.1%		
	6 (740)	498	13.92 ± 4.00			
Enhanced climber-cutting	1 (0)	595	5.44 ± 0.88			
	2 (149)	473	5.45 ± 1.05	33.8%		
	3 (302)	404	7.28 ± 1.34			
	4 (379)	388	7.64 ± 1.37		240.6%	50.0%
	5 (497)	358	11.10 ± 2.30	142.5%		
	6 (740)	297	18.53 ± 4.44			

ABOVE GROUND BIOMASS ACCUMULATION - Table 3 shows the above ground biomass (AGB) accumulation for seedlings planted among the two management practices. In both line planting plots and enhanced climber-cutting plots, biomass accumulation remained constant prior to treatment implementation (measurement interval 1-3) showing that there was no difference between growth rates of planted seedlings. A higher amount of biomass accumulation was seen in the enhanced climber-cutting treatment where AGB accumulation was 56.06% higher post treatment with an overall difference of 81.17%.

SPECIES TRAITS AND RESPONSE TO TREATMENTS - We calculated the standardized major-axis relationships between the difference in species specific growth rates of two treatments. We extracted the wood density, seed mass, carbon to nitrogen ratio (C:N) and specific leaf area (SLA) for all of the studied

species. Wood density varied from 362 - 590 kg/m2, seed mass varied 0.081 - 16.416 g, C:N ratio varied from 2.98 - 3.31 and SLA varied from 13- 31 between the studied species.

Growth response to treatment were inversely related to wood density ($R^2 = 0.0407$, $P = 0.471$), seed weight ($R^2 = 0.1349$, $P = 0.1617$) and C:N ratio ($R^2 = 0.1401112$, $P = 0.1692749$) and positively related to SLA ($R^2 = 0.00097$, $P = 0.9122$). All results show a weak trend. We found seedlings with lower wood densities to show a higher difference in growth rates in the climber-cutting treatment as compared to seedlings with higher wood densities (Appendix 2). Seedlings belonging to trees with higher seed mass showed lower difference of growth rates between treatments as compared to seedlings with higher seed mass (Appendix 3). Species with a high C:N ratio showed lower abilities to respond to the climber-cutting treatment. Where else seedlings with lower C:N ratio showed higher abilities to respond (figure 10). We found seedlings with higher SLA to be able to respond more positively to the climber-cutting treatment in contrast to seedlings with lower SLA (Appendix 4).

Discussion

With a large percentage of the remaining primary forests around South east Asia already receiving the highest protection status, forests conservation efforts has shifted towards degraded and logged forests. With this shift, increased amounts of logged forests are currently being restored using two major silvicultural methods (line planting and enhanced climber-cutting). Here we quantify the potential benefits of the enhanced climber cutting treatment to gain an understanding on its effectiveness as a management strategy. In this study, we aim to assess the implications of this treatment on the growth and survival of restored seedlings and its effects on species composition.

VARIATION IN GROWTH RATES - A current debate among plant ecologists has been centered on how light levels affects the coexistence of plants in densely populated tropical forests. One of the major arguments is that when a species that has a higher growth rate in deep shade, will have a lower growth rate at higher light levels, reviewed by Sack and Grubb (2001). This process is primarily caused by the differences in photosynthetic rates of these different plants that are adapted to deep shade or high light (Givnish 1988). This performance difference between different species and between different light conditions have been theorised as a major driver of species coexistence, where different species partition themselves through a established tradeoff between survival rate in deep shade and growth in high light (Kitajima 1994). The climber-cutting treatment's primary aim is to liberate canopy tree seedlings from increased amount of climbing plants which are capable of intercepting light to the forests floor (Chapter 2). The increase in light levels may cause species to change their growth rates and in the long term, affect species compositions in highly managed forests.

In this experiment we planted a total of 2107 dipterocarp seedlings, monitored them over a 2.6 year period (953 days) and carried out six repeated measurements over this study. We fitted linear growth models to repeated-measured seedlings using linear mixed-effects models and estimated basal diameter size corrected growth rates (SGR) between the two different treatments. Our results showed that the climber-cutting treatment increased growth rates for all species with the exception of one (*Parashorea malaanonan*) that showed a weak decrease in growth in the climber-cutting treatment. We found that species showed difference

in growth rates as a response to the treatment. A total of nine dipterocarp species out of the 16 showed an increase in basal diameter SGR between the two experimental treatments. Seven out of the studied showed little to no difference in basal diameter SGR in the enhanced climber-cutting treatment (figure 4). The majority of species within this similar functional group exhibited positive growth relationships in both high light and low light treatments suggesting that the treatment does not negatively impact studied seedlings by reducing their growth performance for the exception of one insignificant trend.

At both extremes of the growth performance ranks, the fastest and the slowest ranking species retained their position between the two treatments, parallel to studies carried out by Kitajima (1994) and Dent (2009), who both found that rank performance of species does not change along light intensity gradients. However, among the intermediate ranked species, a crossover or rank reversal was found. Overall, eight species were seen to increase in ranking in the climber-cutting treatment with seven species showing a decrease in rank. This rank reversal was seen to be parallel to studies carried out by Sack *et al*. (2001) and Baltzer *et al*. (2007), suggesting that light might play a role in partitioning these species. We found similar results to a shade house experiment where 21 species were tested, Philipson *et al*. (2012) also found that species showed a rank reversal among the different tested light environments. Our findings suggest that there is a small level of specialization to different light environments between our studied species that in turn can contribute to shifts in species composition in the long run.

VARIATION IN MORTALITY - Overall our study showed that there were no differences in mortality rates for the different treatments. Probability of mortality of seedlings however, was seen to decrease with increased light levels between both treatments. Eight of the 16 studied species showed a weak trend of having a higher probability of mortality in the line planting method. This result suggests that although there is not a strong difference between treatments, the enhanced climber-cutting method creates more favorable conditions to reduce the probability of mortality for these eight species. Our findings are parallel to those found by Bloor and Grubb (2003) that also reported no differences in mortality of seedlings among their light treatments (0.4-2.0% and 0.8% full sun) however, the lowest light condition (0.2% full sun) showed to increase mortality rates of their studied species. Our result of low differences between treatments could have

arose because all species tested were predominantly shade tolerant species and that difference in light levels from 4.9% to 7.2% were not high enough to subject these species to intolerable light levels. Studies that do show a difference in mortality rates between high and low light levels often use species with contrasting regenerative strategies which include both late successional species and pioneer species as carried out by Kitajima (1994) and Walters *et al*. (2000).

GROWTH AND MORTALITY TRADE-OFF - The trade-off between seedling growth rates and mortality rates is considered to be one of the most established axis of life history variation among forest tree species (Grubb 1977, Pacala et al. 1996, Wright 2002, Poorter & Kitajima 2007). In this study we see that the trade off is capable of shifting between the two treatments tested. We see a weak negative trade-off with seedlings growing in the standard line planting method (figure 6 above). In the climber-cutting treatment however, we see a weak positive trade off (figure 6 below). Our results however are too weak to show any major tradeoffs between the growth of our study species in both treatments. This weak result would be primarily caused by the light levels created by the enhanced climber-cutting treatment (chapter 2), which did not subject species to extreme conditions (i.e. extreme dark and extreme high light environments).

SEEDLING RANK SHIFTS - Seedlings that were top of the rank in growth performance in one treatment did not drop to the lowest ranking in the increased light conditions. However a small amount of intermediate ranked species did show a performance rank shift in terms of growth (table 2). Out of the 16 species studied six showed a high rank shift (>7 rank orders). Three species showed a higher preference (based on performance) in the enhanced climber-cutting treatment which included *Shorea argentifolia*, *Shorea gibbosa* and *Shorea beccariana*. These three species respectively showed an increase in performance by 6, 8 and 7 rankings respectively in the enhanced climber-cutting treatment. *Shorea leprosula*, *Parashorea malaanonan* and *Parashorea tomentella* however, showed preference for the line planting method by showing a fall in rank orders by 7, 10 and 7 respectively. Our findings indicate that at least six out of the 16 species studied show a strong preference towards each treatment.

SEEDLING TRAITS AND ABILITY TO RESPOND TO TREATMENTS - We tested how seedling traits of the studied species would respond to the two tested treatments in order to determine what plant traits were more favorable for the climber-cutting treatment. We found the strongest relationship to be between species C:N ratio, followed by seed mass, wood density and specific leaf area (SLA). All results showed a weak inverse relationship as the ability for seedlings to respond to the climber-cutting method (difference of growth rate between the line planting method and the enhanced climber-cutting method) with the exception for SLA that had a weak positive relationship. This translates to species that have a higher wood density, will respond to the climber-cutting slower then species with a lower wood density. Our findings run parallel to that of Enquist (1999) who reports that lighter wood densities corresponds to faster growth rates. We found that smaller seeded seedlings (mass), benefited from the climber-cutting treatment.

Our growth rates were size corrected for initial plant size, which would take into account difference in plant size at the start of the experiment (Philipson et al. 2012). However, our results contradict findings by Turnbull (2008) who showed that smaller seeded plants do not grow faster than larger seeded plants when relative growth rate (RGR) is corrected for seed size. This contradicting finding could be because although we tested how seedlings respond rates are dependent on seed size, however our growth rates were size corrected for initial plant size (as opposed to seed size). We also found that the seedlings with a higher C:N ratio were found to show a greater response rate as compared to seedling with lower C:N ratios. Seedlings with higher SLA responded more positively to the climber-cutting treatment as compared to seedlings with lower SLA. This is caused by the fact that a lower SLA often leads to a reduced unit area per unit plant mass (LAR), which then causes a lower relative growth rate (RGR) when a plant increases in size (Lambers et al. 1998).

IMPLICATIONS FOR SPECIES COEXISTENCE - Performance trade-offs remains one of the key mechanisms that control species coexistence in diverse tropical systems. These differentiations in niches play an important role in how these forests retain a high level of diversity and maintain coexistence. Results from this study contributes to the already existing studies in a range of different tropical forests and shows that shade tolerant species do not respond to light equally and thus, exhibits preference to small ranges of light

availability. Our findings that species show a crossover in rank performance between treatments indicates that some species have a higher preference for either the line planting treatment or the enhanced climber-cutting treatment (or differences in light levels). Studies investigating how dipterocarp seedlings respond to gap size give a further understanding to what extend of light intensity these seedlings are able to sustain among other shade tolerant climax species. Brokaw (1985) and Tuomela *et al*.(1996) both found that that when canopy gaps exceed 500 m^2, pioneer species tends to take place and therefore managing light levels within the light range (as seen by the climber-cutting treatment) can increase growth of targeted species (dipterocarps) while limiting the establishment of pioneer species.

IMPLEMENTATIONS FOR FOREST MANAGEMENT AND CARBON SEQUESTRATION - Based on the results from this experiment, we have illustrated that the primary intention of increasing seedling growth has proven to be successful with the use of the climber-cutting method. We found overall, all species improved in basal diameter SGR without apparent negative impacts of increasing mortality. In this study, all experimental plants that were used were planted in order to provide an unbiased comparison between the two different treatments. The initial aims of using the climber-cutting method has been proposed as a stand alone method to reduce costs of planting. This can result in successful outcomes providing that a sufficient density of targeted tree species persists in the restored forest. Currently this method has been proposed to be carried out on both unplanted logged forest (where seedling stocks persist) and over forests which has been restored by line planting methods as carried out by restoration projects such as the INFRAPRO / FACE foundation project (Reynolds et al. 2011).

Our AGB calculations show that overall, an increase in AGB hence carbon sequestration does occur with planted seedlings showing an increased in growth rates. However, the initial loss by the elimination of climbers and the biomass they contain should be taken into account in order to calculate the net gain of carbon years after treatment as the seedlings benefit from the increased growth rates. Climbing plants have been estimated to contribute up to 4.5% of estimated above ground biomass in a study carried out in an evergreen forests in Venezuela (Putz 1983) and in S.E Asian lowland dipterocarp forests, densities remain lower compared to Amazonian forests where liana abundance can almost be 24 times higher (2471 stems/ha)

(Pérez-Salicrup 2001). The frequency of when the treatment should be implemented would have to be monitored frequently in order to assessed when the climber-cutting treatment should be carried out. Crude studies looking at the frequency of cutting have shown that shorter cutting cycles (19 years compared to 40 years cycles) can play an important role in liana infestation increasing the growth of targeted tree species (Addo-Fordjour et al. 2013). Detailed studies looking at rates of re-infestation remains key in understanding how to maximize the efficiency of this treatment.

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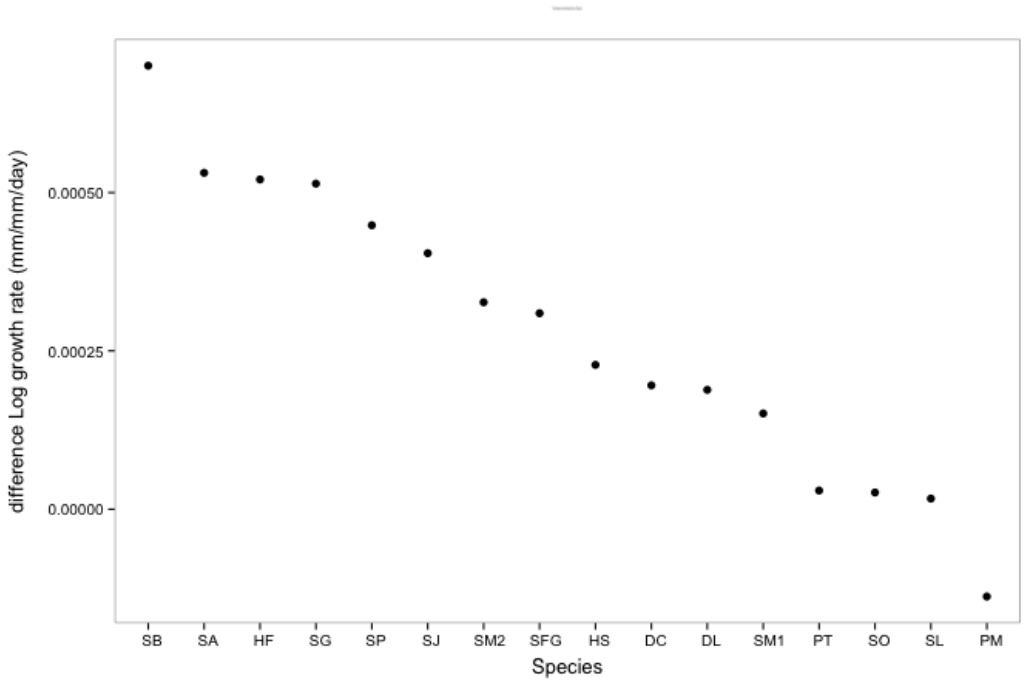
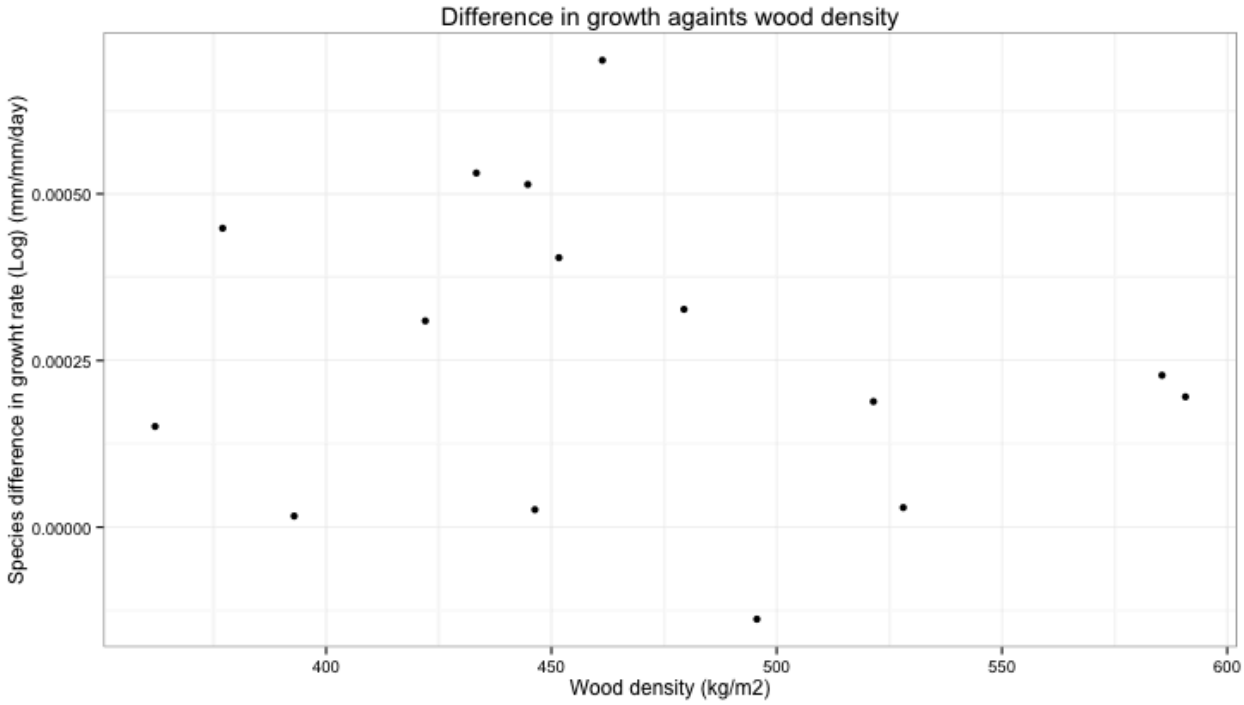
Appendix

Appendix table 1: Significance of fixed effects and interactions (Mixed Model ANOVA) of seedling growth. Bold type indicates significant values ($P < 0.05$).

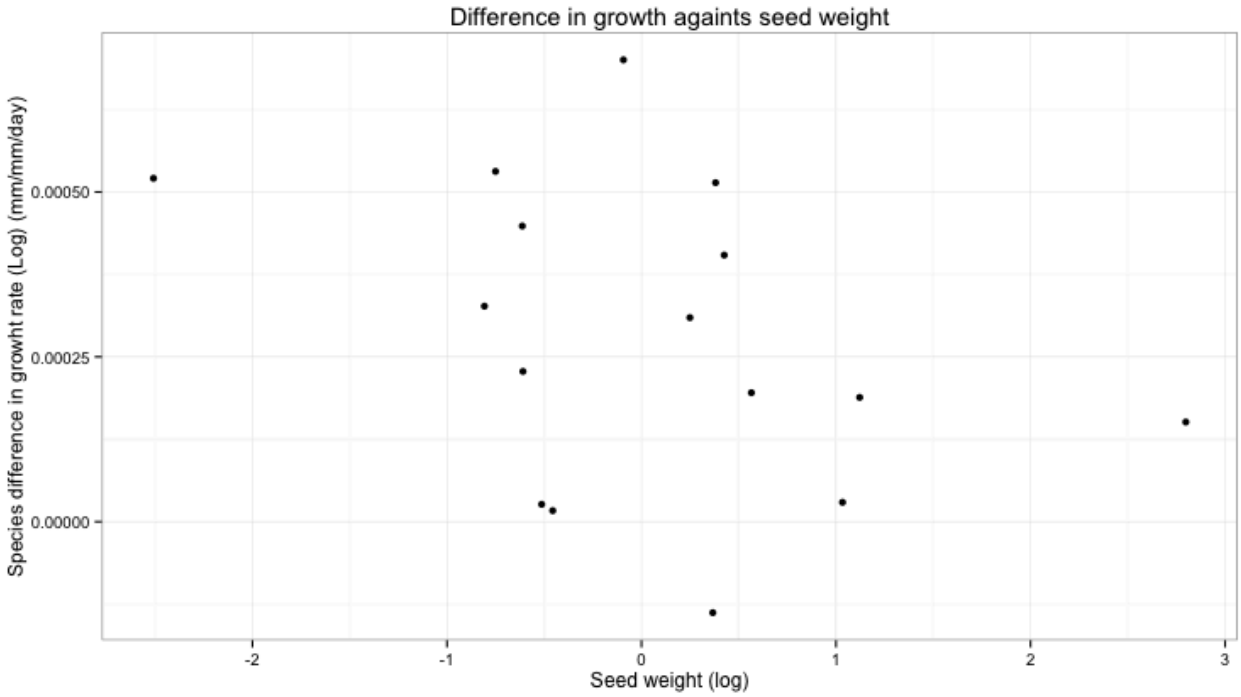
	NumDF	DenDF	F	P
(Intercept)	1	21345	840.6527	**<.0001**
Day (time)	1	21345	977.2445	**<.0001**
Mean canopy	1	21345	9.8604	**0.0017**
Treatment	1	24	0.4843	0.4932
Species	15	1211	17.2638	**<.0001**
Day:Treatment	1	21345	40.8456	**<.0001**
Day:Species	15	21345	2.0381	**0.0104**
Treatment:Species	15	1211	2.0969	**0.0082**
Day:Mean canopy	1	21345	28.1806	**<.0001**
Day:Treatment:Species	15	21345	1.1741	0.2847



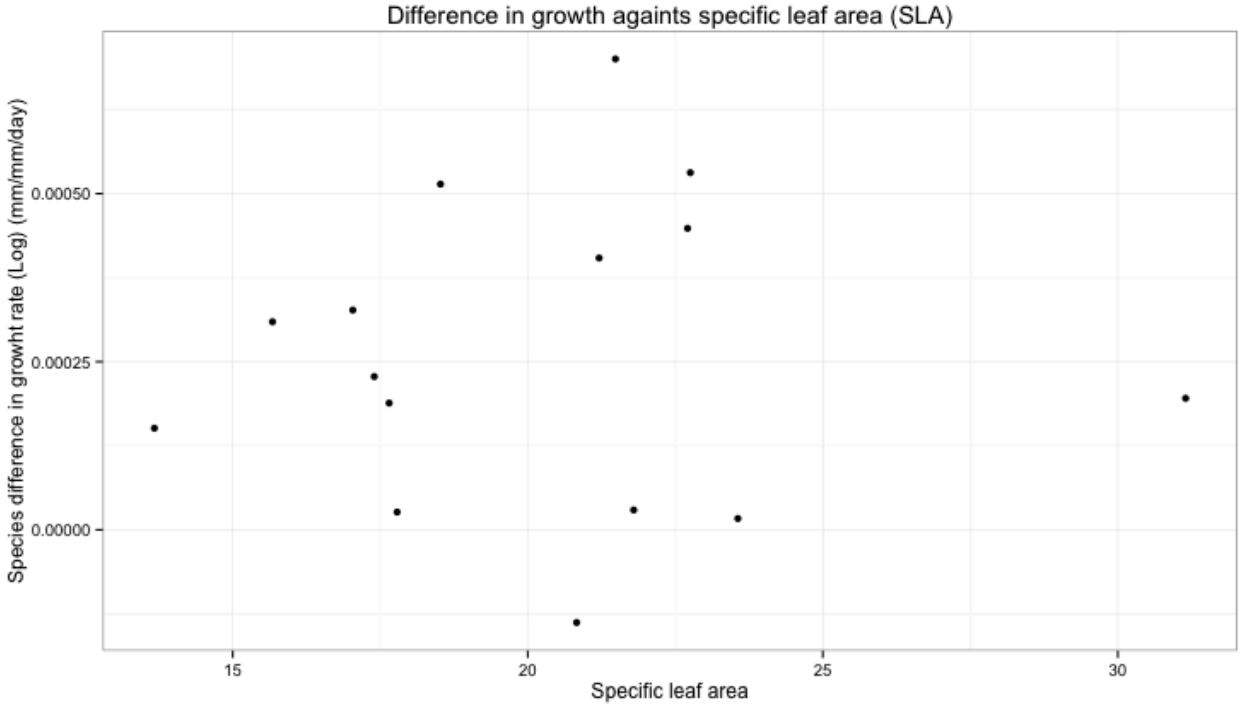
Appendix 1: mean SRGR differences Basal diameter growth rates of 16 dipterocarp seedlings in experiment. Seedlings ordered from left to right based on differences in growth rate.



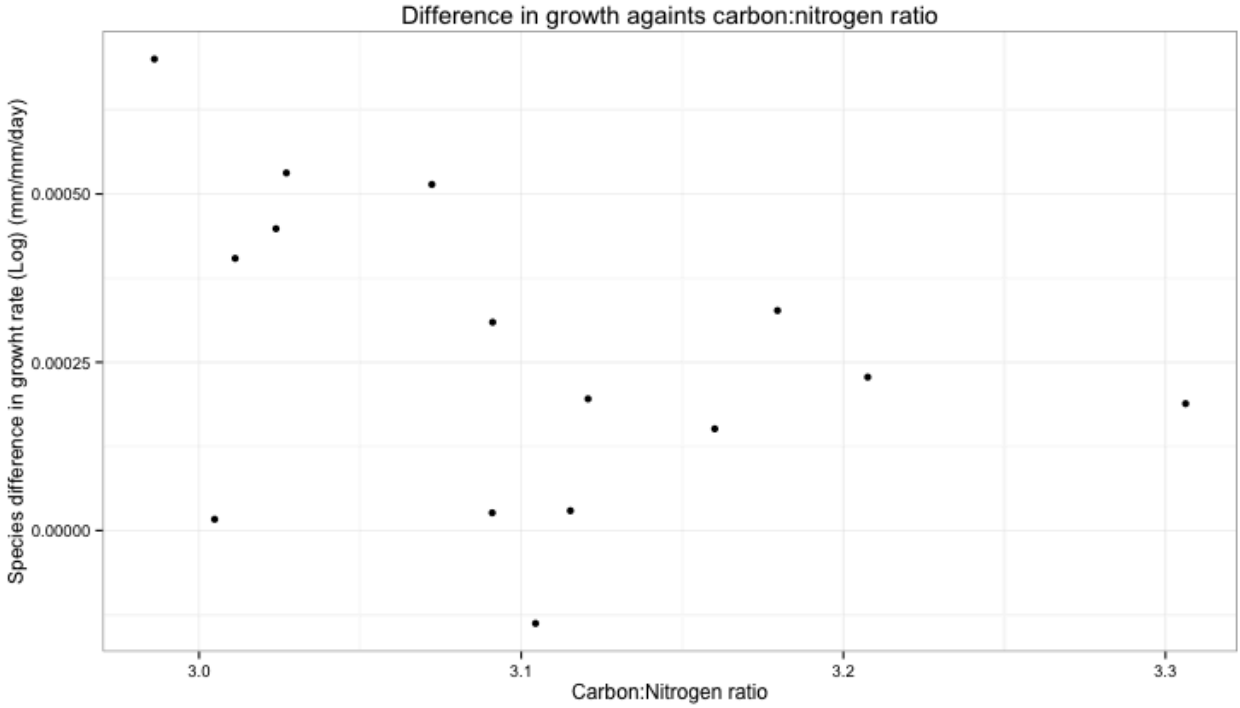
Appendix 2: Relationship between wood density and the ability to respond to enhance climber-cutting treatment (R^2= 0.04074213, P = 0.4706591). Line represents standard major axis regression.



Appendix 3: Relationship between seed weight and the ability to respond to enhance climber-cutting treatment (R^2=0.1348688, P =0.1617264). Line represents standard major axis regression.



Appendix 4: Relationship between specific leaf area (SLA) and the ability to respond to enhance climber-cutting treatment (R^2=0.0009722294, P = 0.9121628). Line represents standard major axis regression.



Appendix 5: Relationship between carbon:nitrogen ratio and the ability to respond to enhance climber-cutting treatment (R^2=0.1401112, P =0.1692749). Line represents standard major axis regression.

Appendix table 2: Spearman's (and Pearson's) table of coefficients.

	Growth differences	Wood density	Seed mass	C:N Ratio
Wood density	-0.16 (-0.20)			
Seed mass	-0.43 (-0.22)	0.17 (-0.33)		
C:N Ratio	-0.36 (-0.37)	0.50 (0.50)	0.27 (0.28)	
Specific leaf area	0.09 (0.03)	0.10 (0.34)	-0.11 (-0.41)	-0.55 (-0.40)

Chapter 4: **Changes in arthropod biomass with intensification of managed lowland dipterocarp forest**

Changes in arthropod biomass with intensification of managed lowland dipterocarp forest

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Abstract

Logged forests dominates 63% of total remaining forest cover throughout South-east Asia. Large scale disturbances such as selective logging have increased the abundance of lianas and climbing bamboo, which limits natural regeneration of these forests. In order to improve regeneration of the climax tropical tree species, large areas are currently being restored using the climber-cutting silvicultural treatment. This treatment aims to reduce tree aboveground competition by the eradication of lianas and climbing bamboo however, its implications to arthropod communities have yet to be examined. The forest canopy provides an abundance of space and resources which arthropod communities depend on, where large percentages of arthropod diversity can be found within the crowns of canopy trees and within epiphytic plants. Here we investigate the effects of removal of lianas and climbing bamboo on arthropod biomass in a large scale experimental restoration project in the Malaysian state of Sabah, Borneo and test the following hypothesis: (1) does the reduction of climbing plants cause a decrease in arthropod biomass and (2) how quickly does arthropod biomass return to control volumes following cessation of climber-cutting. We found that four ordinal groups were affected by the climber-cutting treatment. Blattodea (cockroaches) showed an increase in biomass by 388% and Hymenoptera - family: formicidae (ants), decreased by 45% in biomass when compared to pre-cutting (control) samples. Both groups did not return to control biomass volumes at the end of the study period (4 months post-treatment). Hemiptera (bugs) and Coleoptera (beetles) biomass increased by 31% and 59% respectively one month after treatment however, returned to control levels four months after treatment had been implemented. The remaining ordinal groups surveyed did not show any change in biomass.

Introduction

The lowland tropical forest of South-east Asia is one of the most biodiverse terrestrial regions. Tropical forests provide habitat space for a range of plant and animal life, and are responsible for important roles such as the regulation of local and global climate patterns (Chazdon 2008; Noble & Dirzo 1997; Bonan 2008). In key tropical hotspots, these forest can hold up to 34,000 endemic plants (27% of all plant species in tropical forest, 13% of all plant species worldwide) and estimated 700,000 endemic animal species (Myers 1988). Extensive exploitation of the commercially valuable timber has left these forests in a disrupted state, but their capabilities to retain biodiversity remains high after logging (Edwards et al. 2011). Tropical forests of South-east Asia are currently listed as vulnerable landscapes primarily caused by their levels of degradation and climatic instability predicted for the region (Watson & Herring 2012).

In the Malaysian states of Sabah and Sarawak on the island of Borneo, 80% of land cover has been affected by logging operations between 1990 and 2009 (Bryan et al. 2013). Intact forest in the state of Sabah is confined to protected land that make up just 8% of total land cover leaving a large proportion of land coverage destined for rehabilitation (Reynolds et al. 2011). Methods commonly used include enrichment planting, where seedling stocks of canopy trees have been depleted, or by silvicultral treatments such as climber-cutting when seedlings stocks remain (Moura-Costa et al. 1994; Chan et al. 2008).

Densities of liana and climbing plants have been shown to dominate logged-over forests and are one of the main limiting factors contributing to the disruption of forest regeneration (Pinard & Putz 1994). Increase in liana densities have been seen throughout the tropics and has been caused by a range of factors including an increase in evapotranspirative demand, increase in forest disturbance, turnover changes in land-use including fragmentation and the elevation of atmospheric CO_2 (Phillips et al. 2002; Schnitzer & Bongers 2011; Wright et al. 2004). The climber-cutting method aims to reduce above ground competition that climbing plants such as lianas and vines impose on dipterocarp seedlings in logged forests. The Sabah Forestry Department has been increasing efforts to restore logged forests in the recent years in order to trade carbon credits and provide stocks for future timber harvesting operations. Following the states forestry reports, a total of 17,490

hectares of forest from 2007 to 2011 have been treated with the enrichment planting method and a further 130,351 hectares of forest from 2006 to 2007 have been rehabilitated using the climber-cutting method (Sabah Forestry Department). The climber-cutting silvicultral method has vastly gained popularity amongst landowners and by the Forestry Department of Sabah for improvements in survival and growth of lowland canopy tree species (chapter 3) including its cheap application costs if substantial amount of desired species persists. Lianas however play significant roles in forest dynamics. In the lowland forests, lianas can constitute up to 40% of woody stems and make up more then 25% of woody species, contributing to a large amount to forest leaf area and biomass (Gerwing & Farias 2000). The removal of this group of plants may cause disruption to canopy arthropod communities that have yet to be evaluated and the loss and reductions in these forested systems may have unforeseen consequences that we have yet to examine (Basset 2001).

Arthropods comprise of a large proportion of the faunal biomass in tropical systems (Basset et al. 2012) and are important contributors to ecosystem functioning (Janzen 1987) that include plant pollination, maintenance of species by herbivory and soil production by decomposition. Arthropod biomasses are important parameters for population studies and are used for the estimation of energy and mineral transfer, and predator-prey relationships (Ganihar 1997). In the highly stratified tropical rainforest, arthropods are vertically distributed (Dial et al. 2006), where the forest canopy provides an abundance of space for which arthropod communities survive. A large percentages of arthropod diversity can be found within crowns of canopy trees and within epiphytic plants (Ellwood et al. 2002).

The structural complexity of tropical forest also plays a major role in supporting arthropod diversity. Vines and climbing plants play a major role in canopy connectivity where they provide linkages between canopy trees for arthropods such as ants (Yanoviack 2012). In the lower canopy (0-20 m), a study looking at the removal of canopy habitat-space created by litter trapping systems (marasmiod fungi) have illustrated that up to 70.2% of arthropods abundance was loss (Snaddon et al. 2012). Past studies that have investigated the role of canopy trimming on litter invertebrates have shown that the opening of the canopy causes a reduction in biomass and diversity levels (Richardson et al. 2010). While the manual eradication of climbing plants using the climber-cutting method is capable of increasing canopy openness by 47%, and increasing levels of litter

by 17% (chapter 2), the effects on canopy arthropods still remain unknown.

This study investigates the effect of the climber-cutting treatment on arthropod biomass. We test the following hypothesis: (1) does the eradication of climbing plants and thus habitat space cause a decrease in arthropod biomass and (2) how quickly does arthropod biomass return to control volumes following cessation of climber-cutting.

Methods

STUDY SITE - The study was conducted on the Sabah Biodiversity experiment (SBE), located in the Malua Forest Reserve (N05°05'20" E117°38'32" 102 m.a.s.l) on the eastern region of the Malaysian state of Sabah, Northern Borneo. Forest in this region consists of logged over lowland mixed dipterocarp forest. Although often considered aseasonal, severe drought periodically occurs, influenced by the El Niño Southern Oscillation (ENSO) and has been recorded in 1986 - 87, 1991 - 94, 1997 - 98 and in 2010 (Bischoff et al. 2005). Annual precipitation recorded at the field station averaged at 3000 mm / year, with an average temperature of 25.5°C. Soil in the region is characterised as orthic acrisol (pH < 6) with a base saturation of 81percent (Hector et al. 2011). The SBE consists of 124, four-hectare plots treated with different planting diversities. The plots are in 2 blocks (southern block (block 1) and northern block (block 2)) -with the main west-logging road dividing the block replicates. The diversity planting treatments of the experimental plots include: 12 unplanted control plots, 32 monoculture, 4 species and 16 species mixture plots (96 plots) and an additional, 16 16-species mixture plots treated with enhanced climber-cutting treatment (see (Hector et al. 2011) for experimental setup).

COLLECTION PLOTS & Climber-Cutting - The southern block was selected for this study. Out of the southern block the 16 species plots were treated with Enhanced Climber-Cutting (ECC) treatment. Seven randomly selected 16-species plots and 16-species ECC plots were selected to give a simple balanced randomized design with two treatments (n=14) (figure 1b). The ECC treatment was implemented from 8 July 2011 - 23 July 2011, following methods carried out by the Sabah forestry department. All woody vines including climbing bamboo (*Dinochola* spp.) and lianas with a basal area larger then 1 cm within ECC experimental plots were manually cut. Climbing plants were manually eradicated at the base of sprouting stem with the use of machetes/parang and were also cut additionally at 1.3 m when clumps were encountered.

INVERTEBRATE COLLECTION - Arthropod canopy samples were fogged prior and posts climber-cutting treatments. Sampling took place between May to December 2011 in three sampling periods; Pre-cutting sample 1: May 05 - 11, post cutting sample 2: Aug 04 - 11 and 3: November 15 - December 8. Sampling sites

were located at the centre of experimental plots 100 m from plot boundaries. Four 1 m² fogging trays were suspended 1.3 m above the forest floor. Each tray was attached to collection funnel containing 70% ethanol. A Swing-fog (Swingtec GmbH, Germany), fogging machine was used containing pybuthrin 33BB non-persistent insecticide . Insecticide fogging was carried out between 07h00 to 09h00 in order to minimise influences of diurnal factors of the arthropod community (Basset 2001) and when wind conditions are at a minimum to prevent insecticide fog from being blown by wind (Turner & Foster 2008). The canopy was then fogged for a total of two minutes, and trays were left standing for one hour to allow insects that had not immediately fallen to be collected. Height of fog ranged from between 15-20 meters.

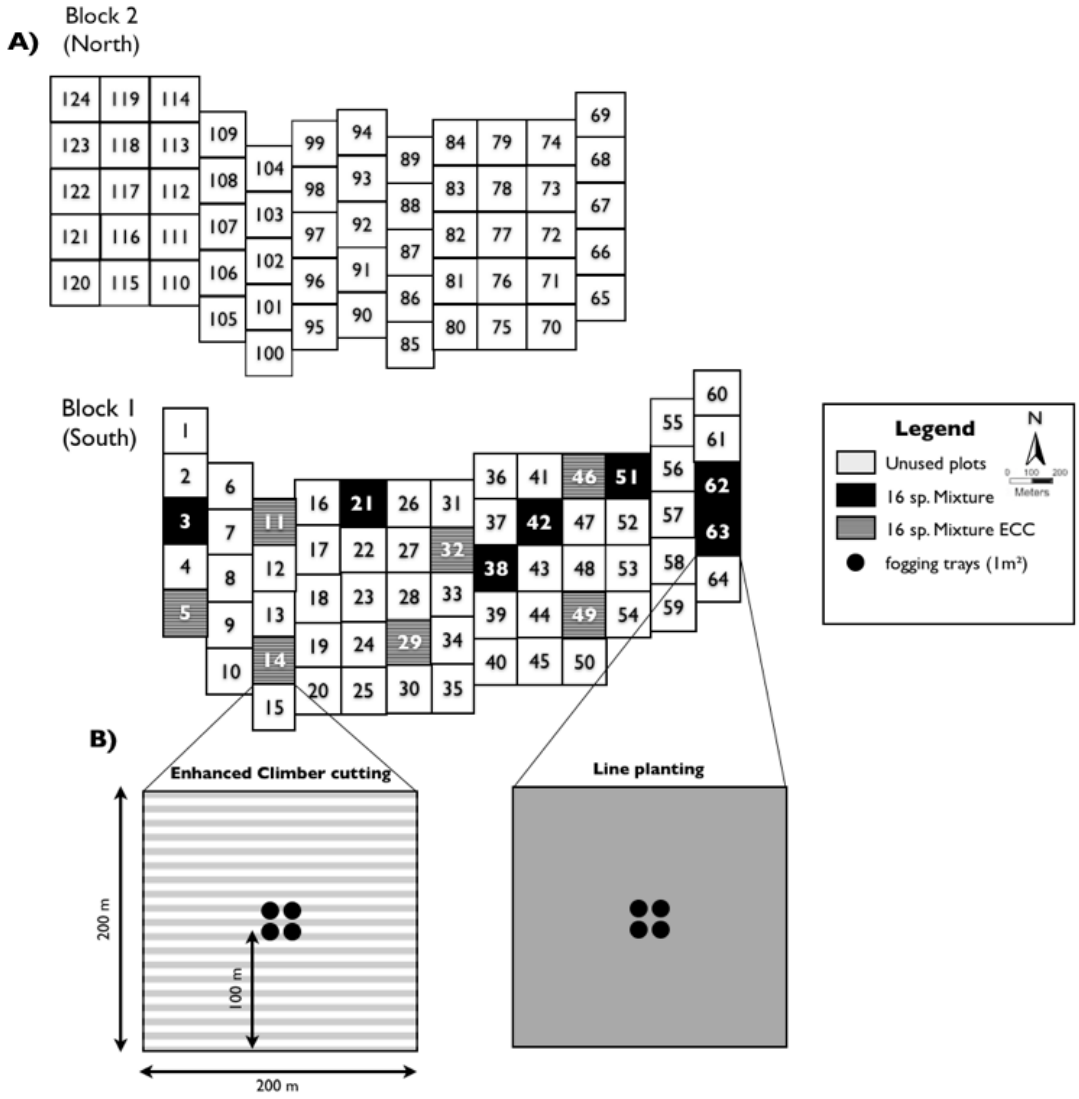


FIGURE 1: (A) selection of plots within the SBE (n=14). (B) Positions of fogging trays and location within plots.

IDENTIFICATION AND BIOMASS - Sampled arthropods were sorted to the ordinal level, with Hymenoptera were divided into suborders. Wasps were placed in groups belonging to the Apocrita suborder and ants placed into a separate family group. Endopterygote insect larvae and isopods were sorted to grouped of their own categories. All samples were stored in 70% ethanol solution. Samples stored in ethanol were drained and dried at 30 degrees for two hours using a rotational vacuum concentrator (Christian RVA Alpha, Germany). Arthropods were weighed grouped in ordinal levels from respective plots using a microbalance (Mettler Toledo).

STATISTICAL ANALYSIS - Data was analysed using mixed models ANOVAs using the NLME package (version 3.1-105 (Pinheiro et al. 2013), with the software package R (version 2.15.0: R. Core Development Team 2012). The ANOVAs examined treatment effect (Enhanced climber-cutting vs. Line planting), whilst controlling for random effects of experimental plots.

Results

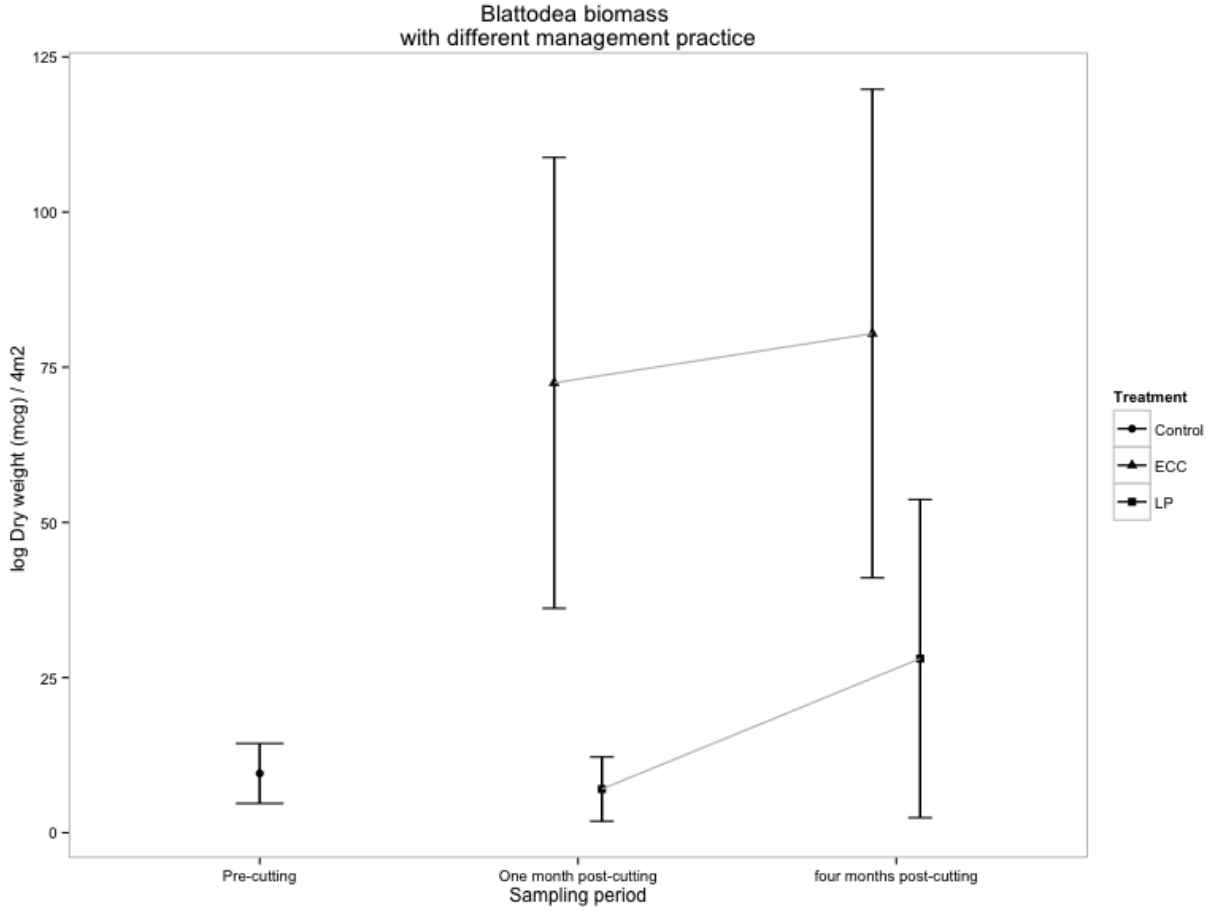
TOTAL ARTHROPOD BIOMASS - A total of 24 ordinal groups of arthropods were sampled over three collection periods. Total biomass (dry mass) from the first sampling period (pre-treatment) was 506.32 μg from the 14 sampling locations (figure 1), these represented an area of 56 m^2 of the forest understory and up to 20 m vertical height. Out of the total, the largest percentage of the sample consisted of Hymenoptera (family: formicidae) which contributed 20.34% to the total biomass (table 1). Phasmatodea and Coleoptera contributed to 15.88 and 15.40% respectively. Remaining ordinal groups contributed in low levels of biomass from between 7.40 - 0.14% (refer to table 1).

ARTHROPOD BIOMASS DIFFERENCE AMONG TREATMENTS - A significant difference was seen in arthropod biomass between treatments (Appendix 1). Pre-treatment values of mean arthropod biomass was equal among all plots with the exception of Blattodea, Hymenoptera (formicidae) and larvae which all showed higher volumes of biomass (with a 83%, 88% and 121% respectively) in enhanced climber-cutting plots as compared to line planting plots (figure 2A, B and Appendix 1). Rainfall and volume of litter prior to fogging played a significant role to volume of arthropods sampled (Appendix 1).

ARTHROPOD BIOMASS OVER TIME - Arthropod biomass varied among different ordinal-levels with respect of sampling time (Appendix 1). Of all the groups sampled during the duration of this study, two groups showed the largest difference and maintained difference four months post treatment. Blattodea (cockroaches) showed an increase in biomass by 388% once the climber-cutting treatment had taken place and remained constant from one month to four months post climber-cutting (figure 2A). Hymenoptera - family: formicidae (ants), decreased by 45% in biomass from pre cutting volumes and remained stable between one month and four months post treatment (figure 2b).

Two orders were affected by the treatment in the short term (one month post treatment), however returned to baseline (pre-cutting) volumes of biomass. This included groups from the Hemiptera order (bugs) and the Coleoptera (beetles) order (figure 3a and 3b). Hemiptera and Coleoptera biomass increased by 31% and 59% respectively one month after treatment had taken place however, returned back to control levels four months after treatment had been implemented. A large amount of arthropod orders were not affected by the treatment however showed a large variation at different fogging intervals (Appendix 2). This included the following

2a)



2b)

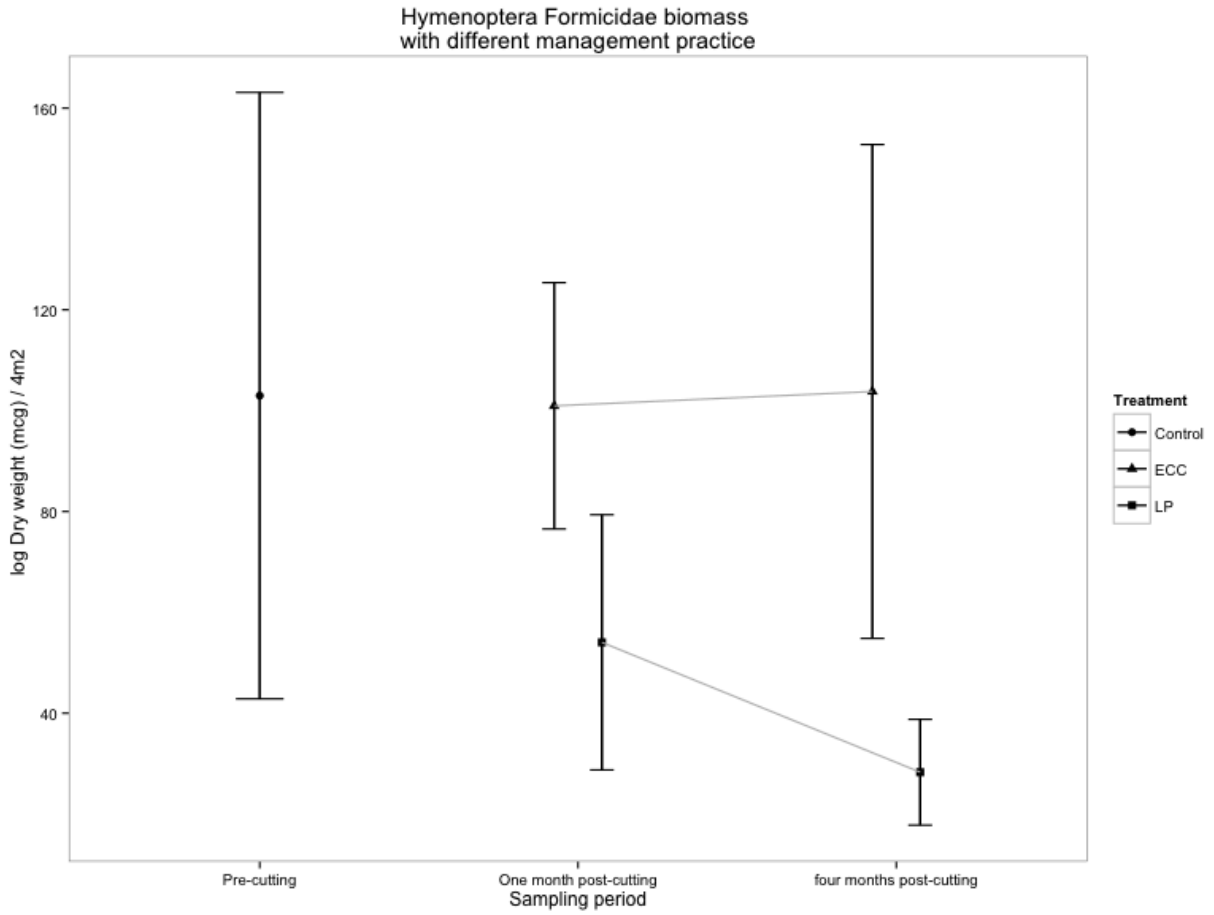
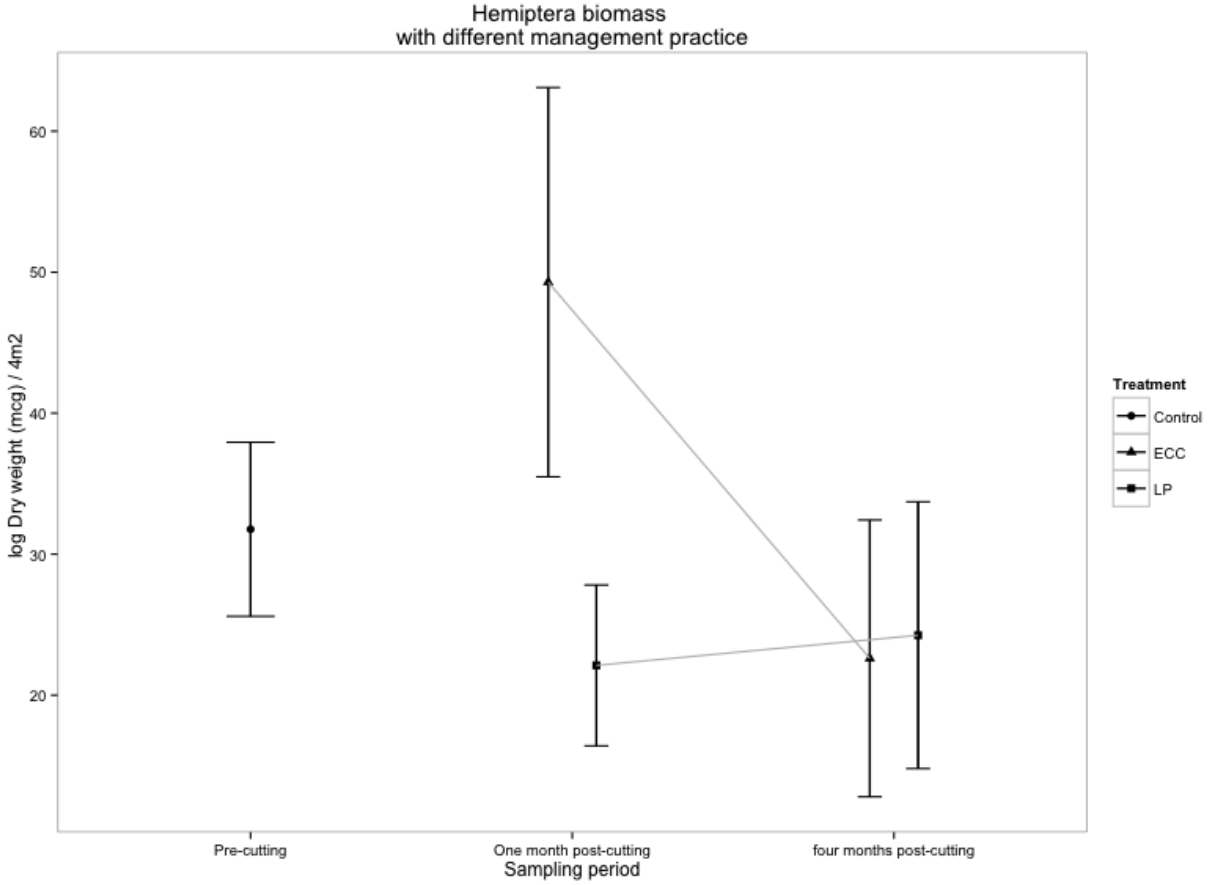


FIGURE 2: Long term effects of climber-cutting on (a) Blattodea and (b) Hymenoptera (Formicidae) biomass (μg / 4 m^{-2} /$plot^{-1}$) over sampling period. Error bars represents ± S.E.

3a)



3b)

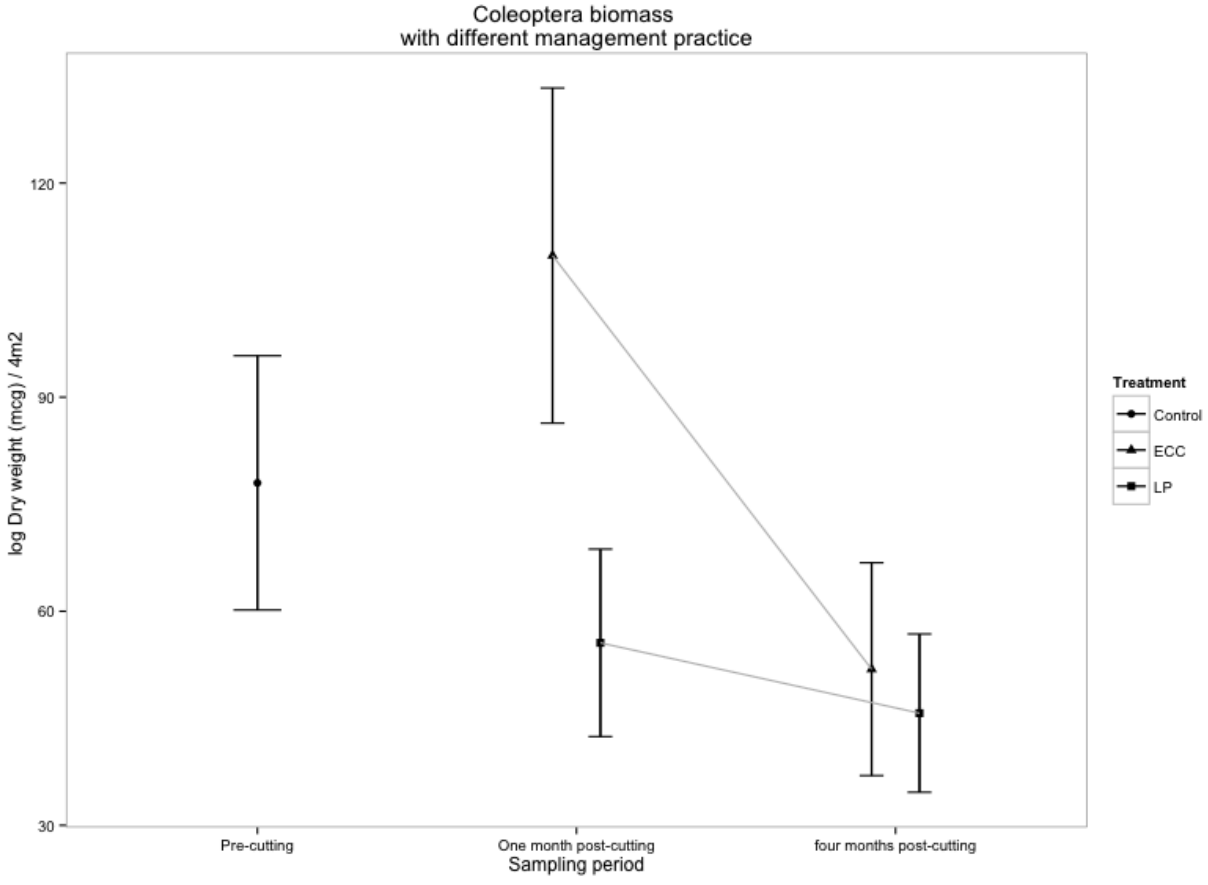


FIGURE 3: Short term effects of climber-cutting on (a) Hemiptera and (b) Coleoptera biomass (μg / 4 m^{-2} /$plot^{-1}$) over sampling period. Error bars represents ± S.E.

orders: Myriapods, Isopoda, Archeogonata, Araneae, Opiliones, Hymenoptera (apocrita), Thysanoptera, Collembola, Diptera, larvae and unidentified arthropods.

Table 1: Mean arthropod biomass (μg) of pre-treatment (control) sample period (n=14). Where N represents number of fogging trays samples were found in.

Ordinal groups	Common names	N	Biomass (μg) / sample (4 m^2)	% total sample
Hymenoptera (family: formicidae)	Ants	14	102.98 ± 60.14	20.34
Phasmatodea	Stick insects	3	80.40 ± 45.21	15.88
Coleoptera	Beetles	14	77.98 ± 17.82	15.40
Mantodea	Mantis	3	37.47 ± 35.18	7.40
Orthoptera	Grasshoppers/ Crickets	13	36.75 ± 8.03	7.26
Hemiptera	True bugs	13	31.77 ± 6.17	6.27
Opiliones	Harvestmen	11	26.71 ± 6.49	5.28
Myriapod	Millipedes/ centipedes	14	23.29 ± 6.35	4.60
Araneae	Spiders	14	18.40 ± 3.66	3.63
Isopoda	Woodlice/pill-bugs	11	15.08 ± 5.46	2.98
Blattodea	Cockroaches	9	9.56 ± 4.83	1.89
Larvae	underdeveloped arthropods	12	9.16 ± 2.14	1.81
Dermaptera	Earwigs	8	5.72 ± 2.60	1.13
Hymenoptera (Sub order: Apocrita)	Bees / wasps	12	5.17 ± 1.19	1.02
Diptera	True flies	13	4.71 ± 0.67	0.93
Blattodea (Isoptera)	Termites	1	4.02 ± 0.00	0.79
Archaeognatha	Jumping Bristletails	12	3.44 ± 1.25	0.68
Lepidoptera	Moths/Butterflies	3	3.27 ± 2.68	0.65
Other	Leeches/snails	1	2.88 ± 0.00	0.57
Collembola	Springtails	12	2.27 ± 0.53	0.45
Ixodida	Ticks	13	1.98 ± 1.34	0.39
Unidentified	Un-categorised	7	1.54 ± 0.6	0.30
Psocoptera	Booklice/ bark-lice/bark-flies	1	1.05 ± 0.00	0.21
Thysanoptera	Thrips	13	0.72 ± 0.17	0.14

Discussion

Lianas and climbing plants contribute a large percentage to the production of canopy foliage, where they can contribute up to 40% of woody stems (Gerwing & Farias 2000). Large scale disturbance such as logging has caused an increase in favourable conditions on which climbing plants such as lianas and climbing bamboo thrive (Van Der Heijden & Phillips 2009). These vines become a major aboveground and belowground competitor for tree seedlings (Schnitzer & Bongers 2002). The principal method to restore these degraded forest include the mechanical elimination of lianas and climbing plants (the climber-cutting silvicultral treatment) which has become one of the primary methods due to its cost efficiency. Results highlighted in chapter two show that the forest canopy foliage is lost and light level to the forest floor is are increased by this treatment. However, the impacts this treatment has on faunal biodiversity has yet to be explored. Here we test how this treatment has affected different groups of arthropods in the lower canopy (0-20 m). Out of the 20 ordinal groups sampled, two showed short term changes and a further two ordinal groups showed changes that persisted four months after treatment implementation.

SHORT TERM EFFECTS - The climber-cutting treatment affected arthropods belonging to the Hemiptera and Coleoptera orders. The increase in biomass of these two groups of arthropods was seen one month after treatment was implemented. Both groups returned to control levels four months after treatment had taken place. The increase in Coleoptera abundance could be attributed by the increase in dead wood, where fresh stands of dead wood provide food sources for their larvae. Studies in China have found that higher proportion of leaf cover and woody debris have been seen to effect beetle species abundance (Luo et al. 2013). A study looking at the effects of gap creation in an old growth east african forests also showed that Hemiptera abundance increased with disturbance (Borghesio 2012). Newly created leaves caused by the opening of the canopy (Naidu & DeLucia 1998) could increased amount of food source for arthropods belonging to the Hemiptera order as large proportion of members of this group (Hemiptera: Miridae) feed on young leaves (Wheeler 2001).

LONG TERM EFFECTS - We found a further two other ordinal groups that were affected by the climber-cutting treatment. These included arthropods belonging to the Hymenoptera (formicidae) order — ants. Ants decrease after one month after the climber-cutting treatment had taken place. This reduction remained low four months after treatment. Ants often use climbing plants such as bamboo as nest sites (Buschinger et al. 1994), a study looking at arthropods associated with climbing bamboo (*Dinochloa trichogona*) found that up to 28 species of ants and ten species of hemipterans have been found utilising this species (Mezger & Blthgen 2007). Rattan which is a climbing palm that was also removed could have reduced ant biomass. Lepsme (1947) listed that 25 arthropod species have been associated with rattan. The elimination of host plants that some species form mutualistic relationships with are disrupted, causing a loss in biomass of this particular group.

Klimes *et al*. (2012) found that when comparing primary forest with logged forests, forest structure had a larger role in supporting ant diversity compared to plant species composition, suggesting that the loss of climbing plants could further cause a loss in ant diversity. This is supported by findings by Woodcock *et al*. (2011) that showed that selective logging retained overall structure of the forest does not have a large impact on ant communities. However, the loss of such a keystone predator may have consequences in the regulation of arthropod herbivores and may cause a sudden increase in arthropods belonging to the Hemiptera order as seen by our results (figure 3a). In an agroforestry exclusion experiment, ants were found to reduce leaf herbivory and fruit pest damage and provided services such as pollination facilitation (Wielgoss *et al*. 2014). To be able to identify the exact role ants play on the maintenance of prey populations, extensive whole forest exclusion studies should be carried out as described by Klimes *et al*. (2011).

Blattodea (Cockroaches) biomass increased one month after the treatment had taken place and remained high four months after treatment. Rapid and sustained increase of cockroaches could be explained by the sudden increase of litter (as shown in chapter 2). Cockroaches play a major role in soil production and are considered to be important detritus feeders that would benefit from the increase in leaf litter and decaying wood (Adl 2003). This short term increase in cockroaches may have beneficial effects since they are known to provide important ecosystem functions including the break down of organic material that would be

beneficial for the cycling of nutrients for both residual plants and planted seedlings.

LACK OF DIFFERENCE BETWEEN OTHER ORDERS - The treatment affected predominantly the most abundant ordinal groups. Ants dominated the control samples and represented 20% of total sampled arthropods biomass, beetles represented 15%, bugs represented 6%, however cockroaches only represented 1% of the control samples. Targeting our sampling design on less abundant groups could yield changes in their abundance, however the fogging method carried out did not sample smaller groups in such detail. Our results suggest that the only ordinal groups that are dependent on what effects the treatment remains an important factor that can contribute to shifts in arthropod biomass. These are seen to be groups that are directly linked to the treatment affects which include climbing bamboo and rattan. Treatment effects such as the increase in litter production, loss in canopy foliage and increase in amount of dead wood (see chapter two) all play important roles. The increase of leaf litter and woody debris are highly likely to have increased roach and beetle biomass. Specific groups which were not linked to either plants that were eradicated or showed any treatment effects did not show any difference. Our collections also reveal that a high variation in biomass as the different groups showed high changes among sampling periods (see appendix 2). These changes in variation could be caused by seasonal changes and how it affects the microclimatic conditions.

HOW WILL THESE FORESTS RESPOND TO CHANGE - The climber-cutting treatment has shown been to change arthropod biomass of particular groups. The decrease of the predatory groups such as ants could cause some top down effects that we have yet to understand. Herbivore insects are capable of reducing plant populations (Bagchi et al. 2014) however, the increase of herbivores belonging to the Hemiptera order have been shown to quickly return to control levels and so this increase may not cause any long term changes that may become detrimental to the maintenance of floral species. A more detailed look at herbivory of plants right after the climber-cutting treatment will give us a greater understanding on how seedlings would have been affected by the increase in herbivores.

CONCLUSION - Overall the treatment caused a change to only four ordinal groups. Although a small fraction of the total sampled were impacted, these groups represented the most common and abundant

ordinal groups and they contribute to important ecosystem services. We hypothesised that this treatment will casuse a decrese in arthopod biomass, however only found the climber-cutting treatment to have decreased one out of the 20 ordinal groups (ants). Instead, we found the treatment to have increased biomass of several arthropod groups including increased beetles, bugs and cockroach. Out of the four orders that were affected, two quickly returned to control levels, however two remained affected four months after treatment. In order to further explore how this treatment has on both ants and cockroaches, repeated samples should be carried out past four month.

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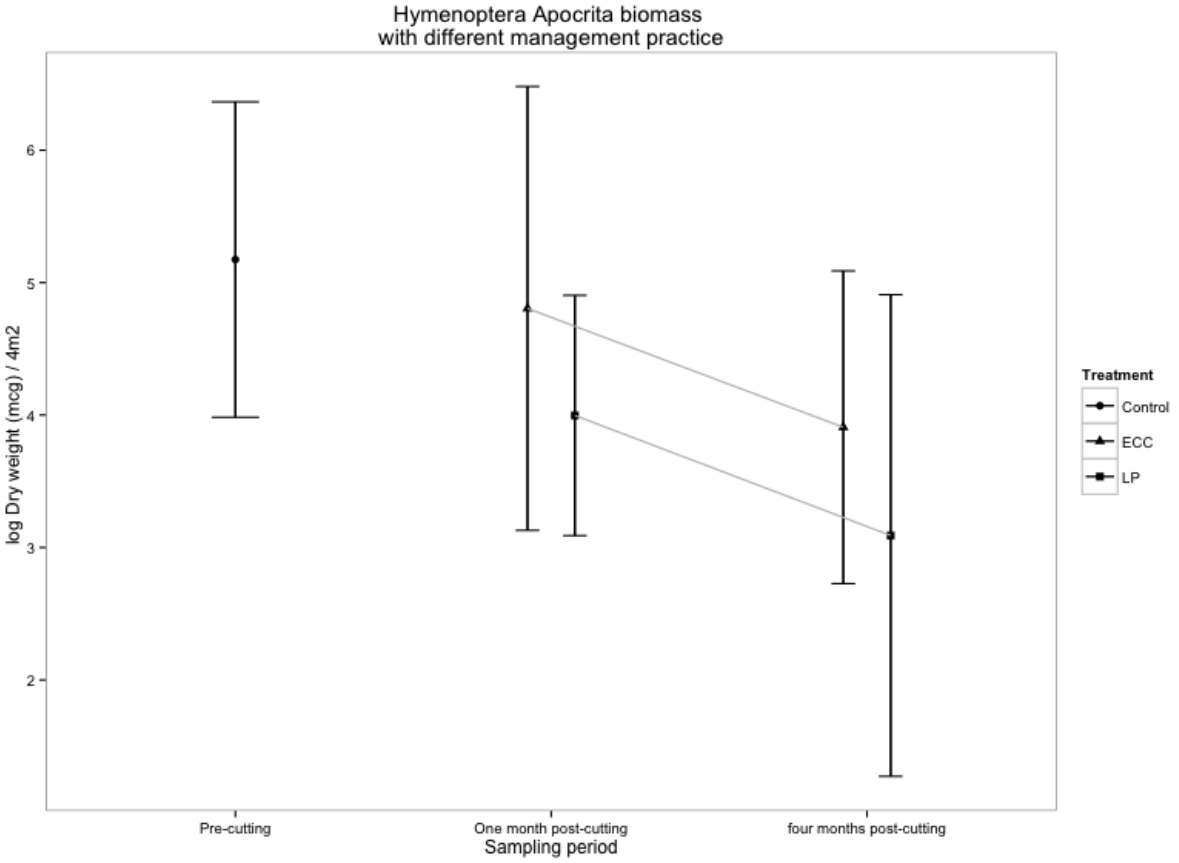
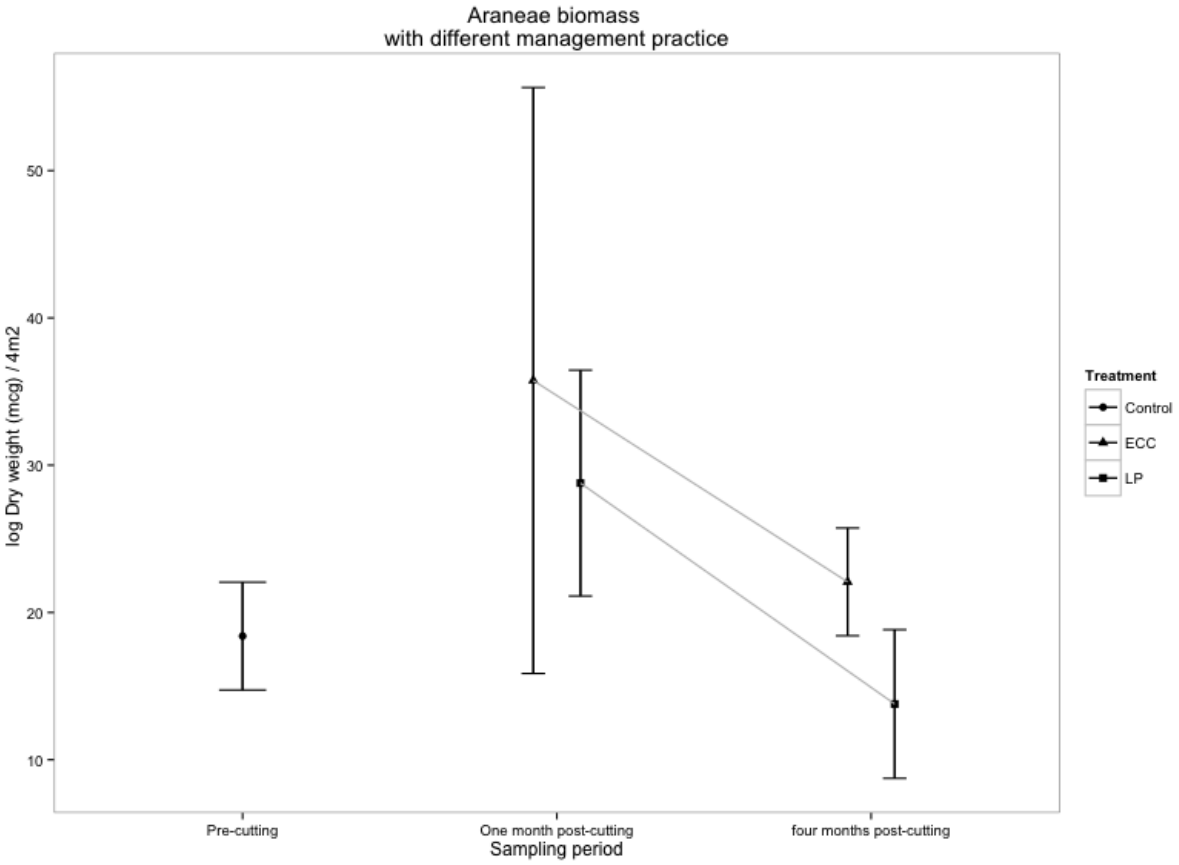
Appendix

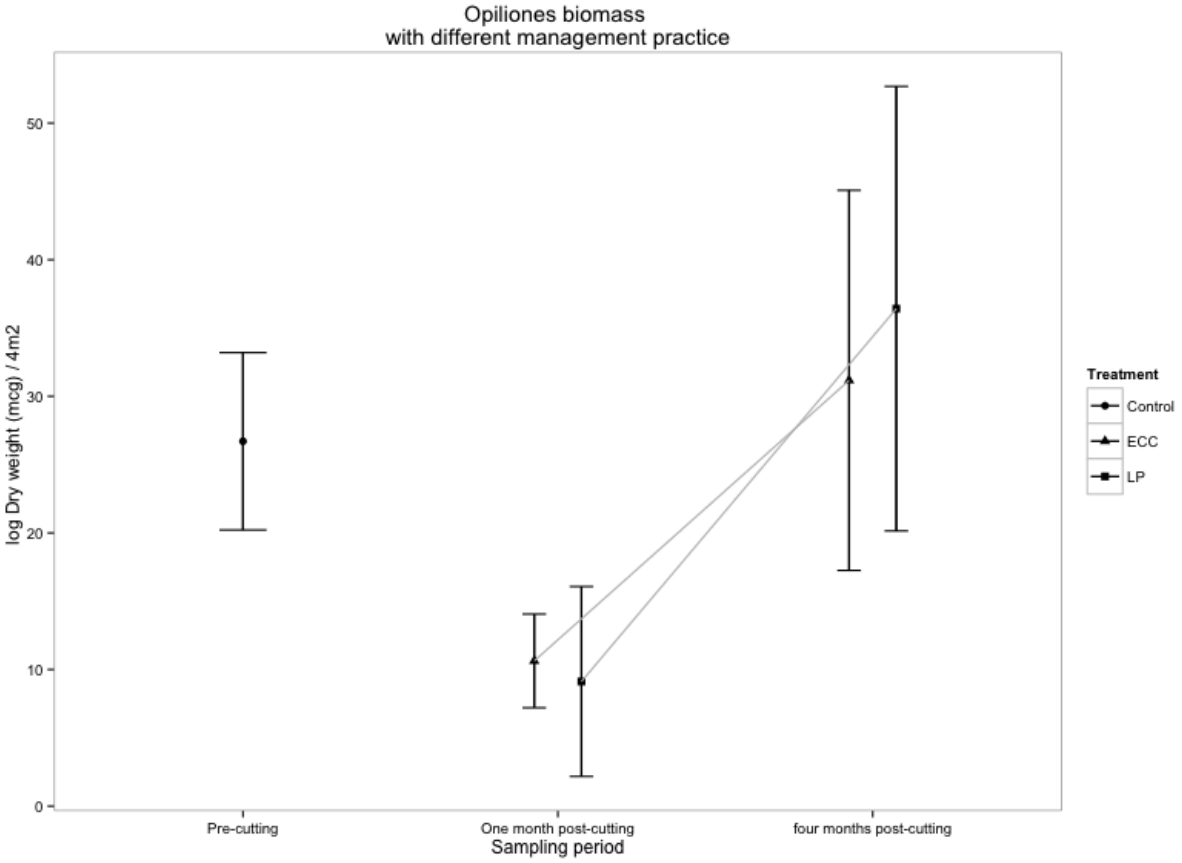
Appendix 1: Significance of fixed effects and interactions (Mixed Model ANOVA) for biomass (dried weight) of arthropods sampled at each plot. Bold type indicates significant values ($P < 0.05$). Data from 56 fogging trays ($1m^2$) Three sampling periods, from precutting values, one month post treatment and four months post treatment.

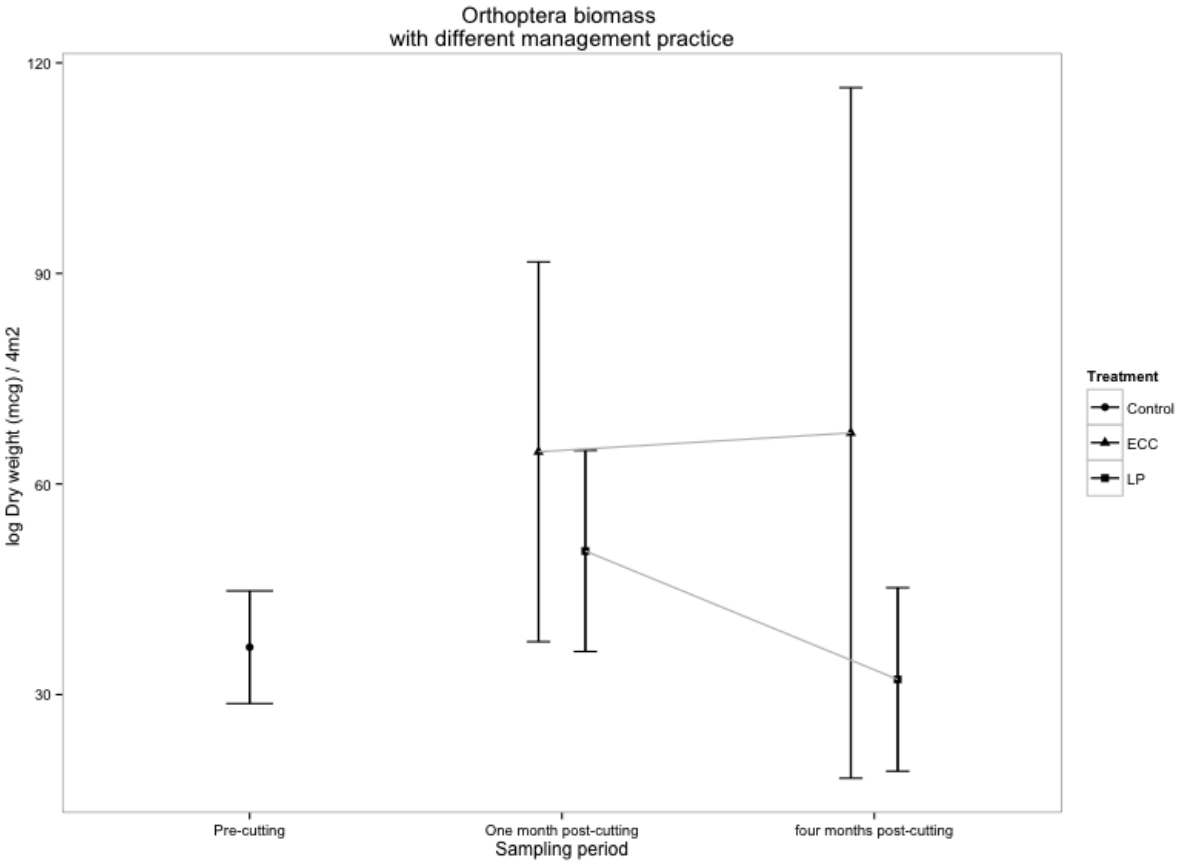
	NumDF	DenDF	F	P
Intercept	1	344	84.53940	**<0.0001**
Fogging sequence (time)	1	344	1.13269	0.2879
Treatment (LP vs. ECC)	1	12	5.60843	**0.0355**
Variable (Arthropod ordinal group)	18	344	9.74062	**<0.0001**
Rainfall prior to sampling (2 weeks)	1	344	4.45418	**0.0355**
Litter fall prior to sampling (1 month prior to fogging)	1	344	7.99388	**0.005**
Fogging sequence (time) X Treatment (LP vs. ECC)	1	344	7.65402	**0.006**
Fogging sequence (time) X Treatment (LP vs. ECC) X Arthropod ordinal group	36	344	1.23264	0.1753





APPENDIX 2: Invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over study period. Error bars represents ± S.E.





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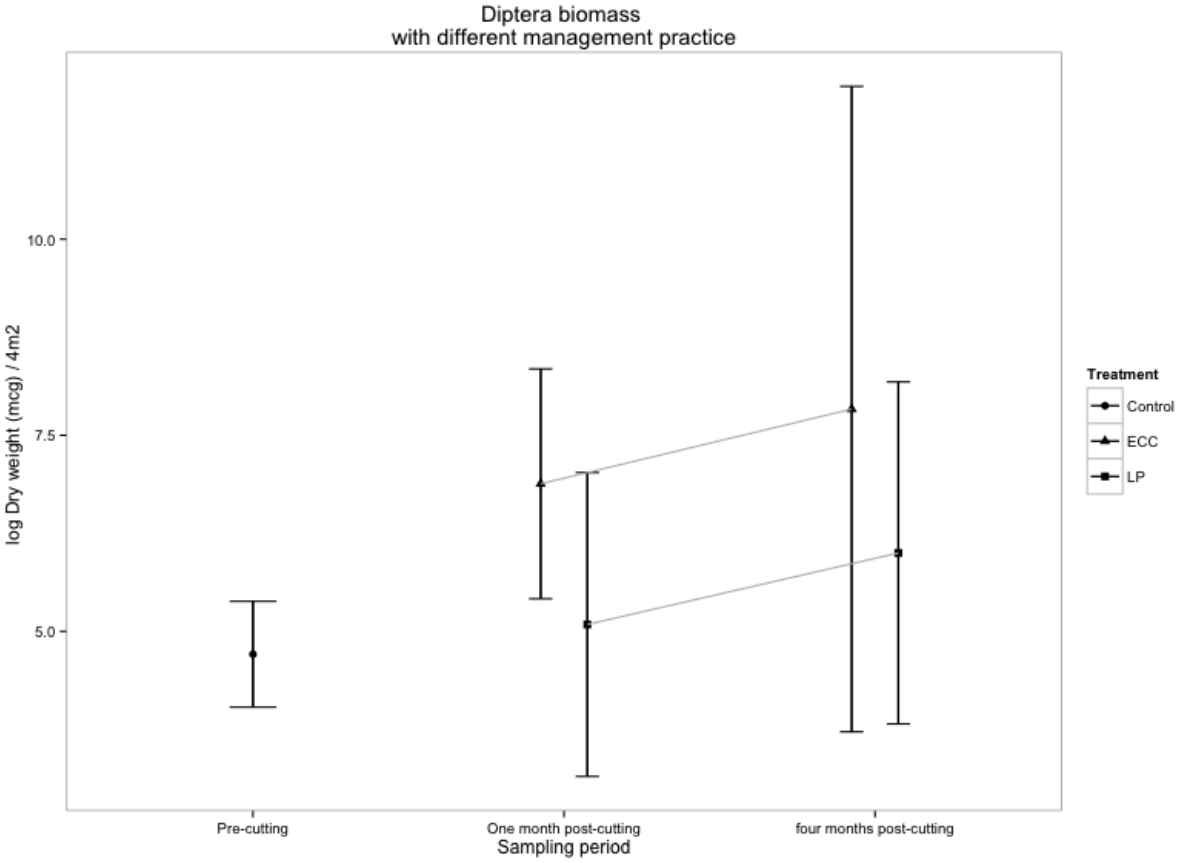
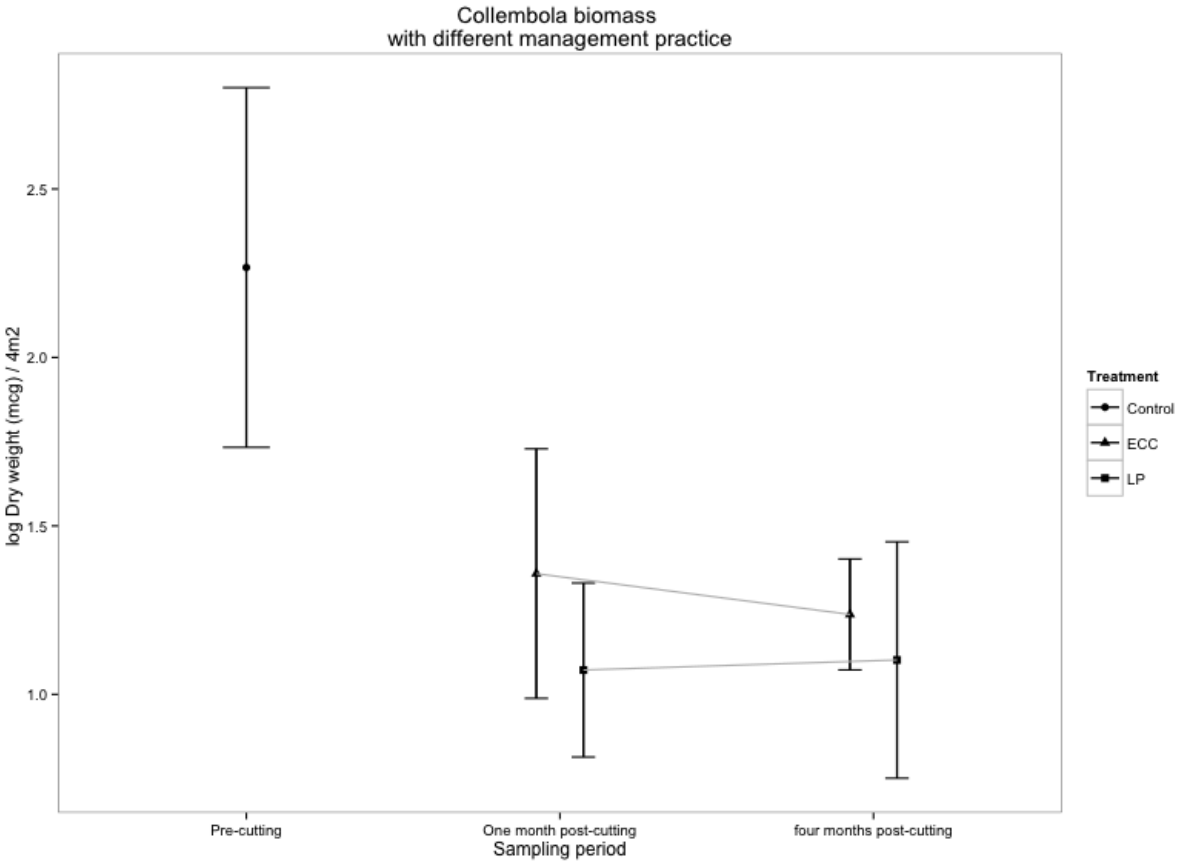
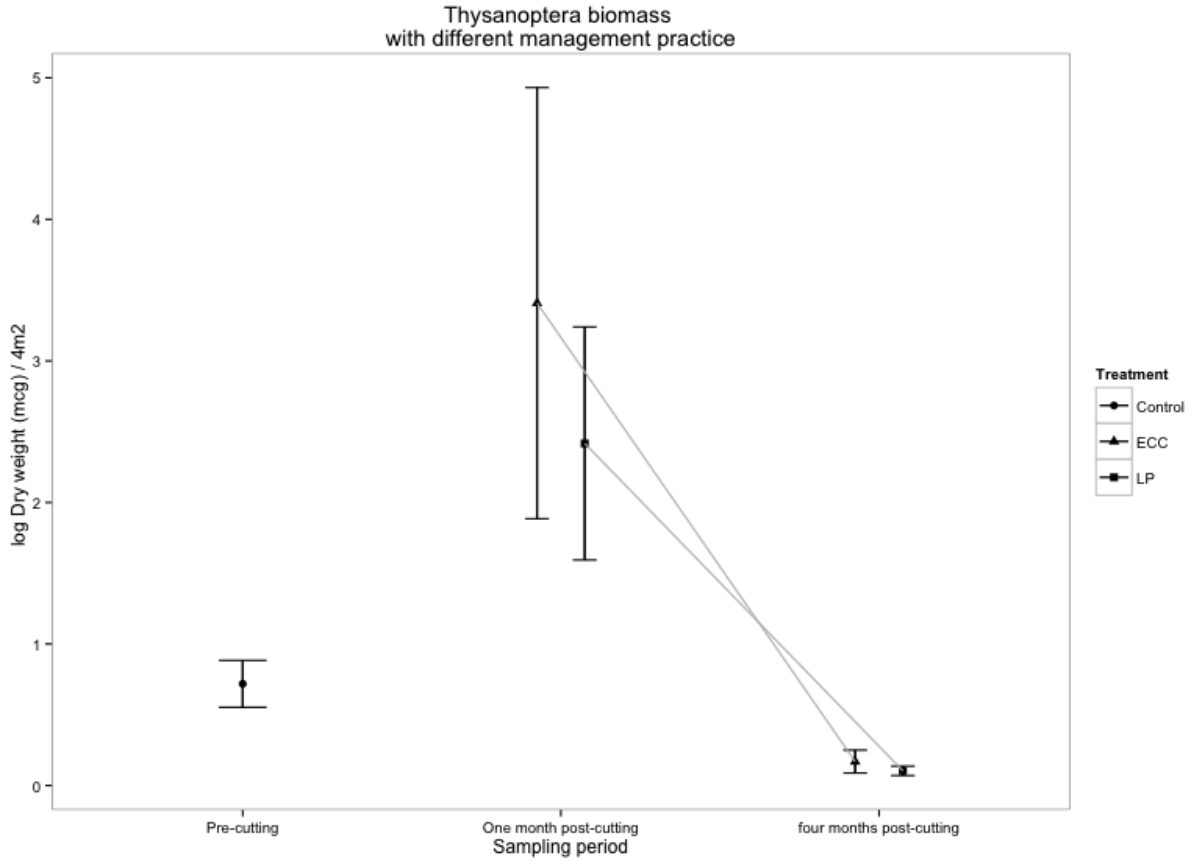
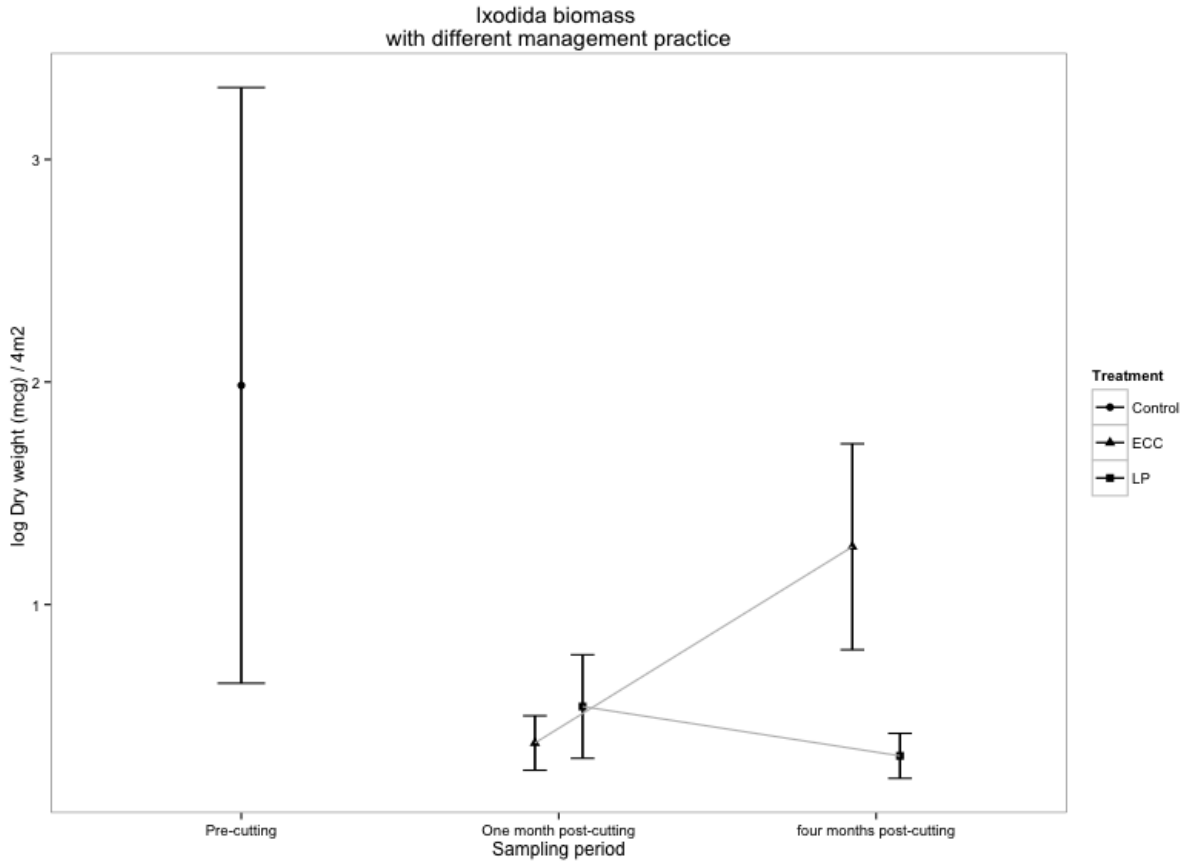


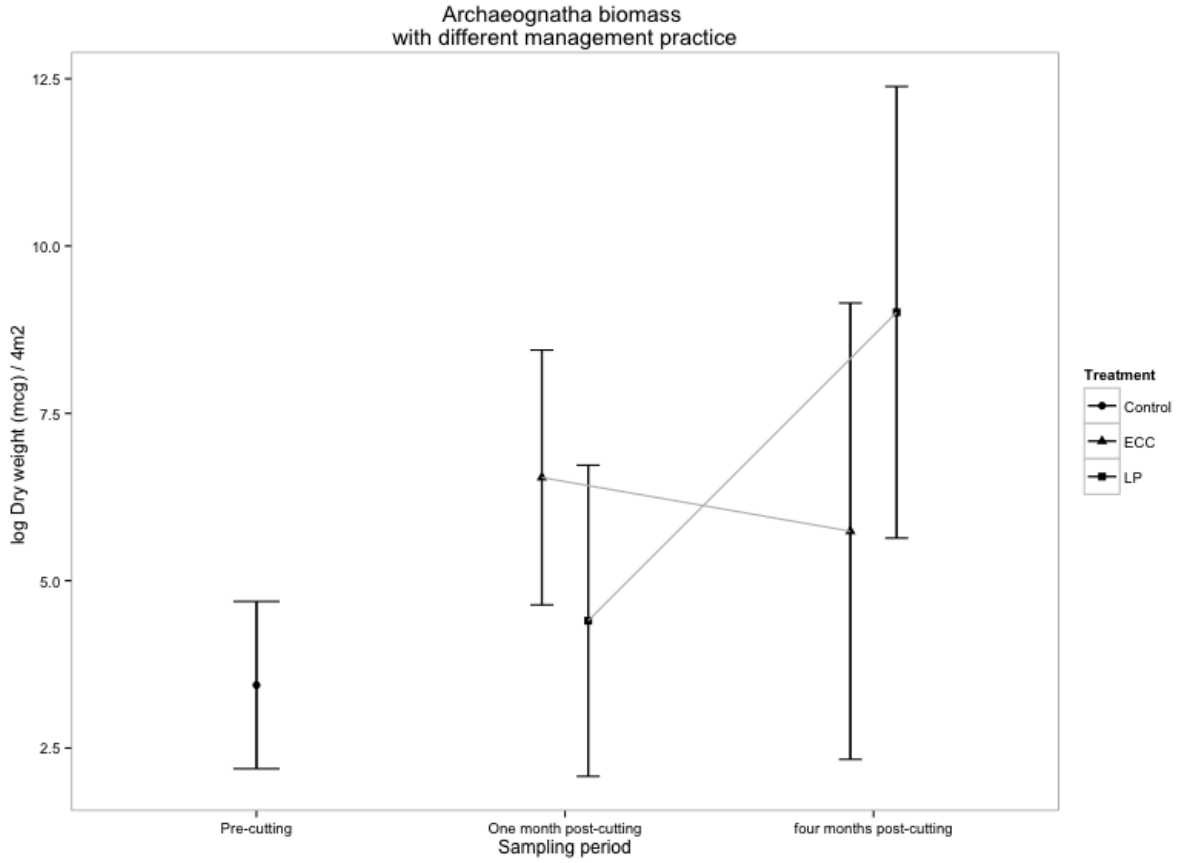


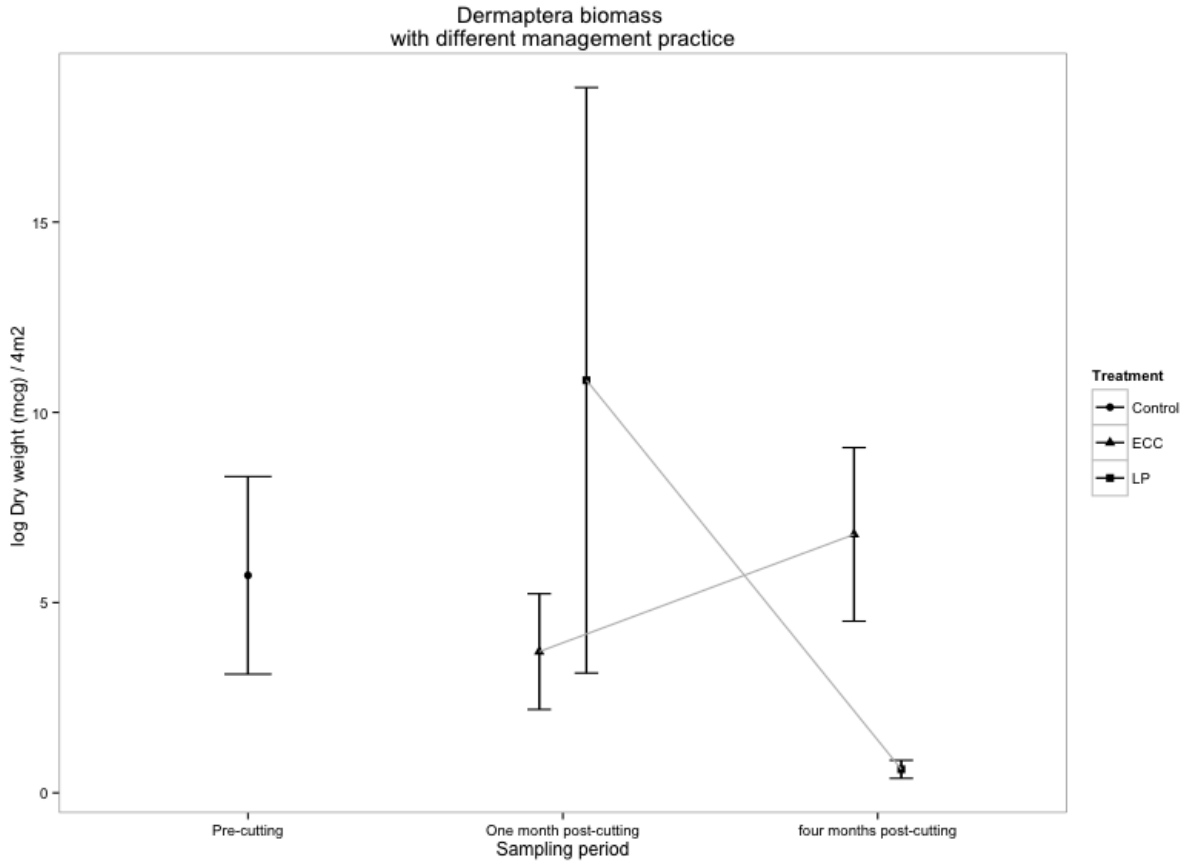
APPENDIX 4: Invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over study period. Error bars represents ± S.E.



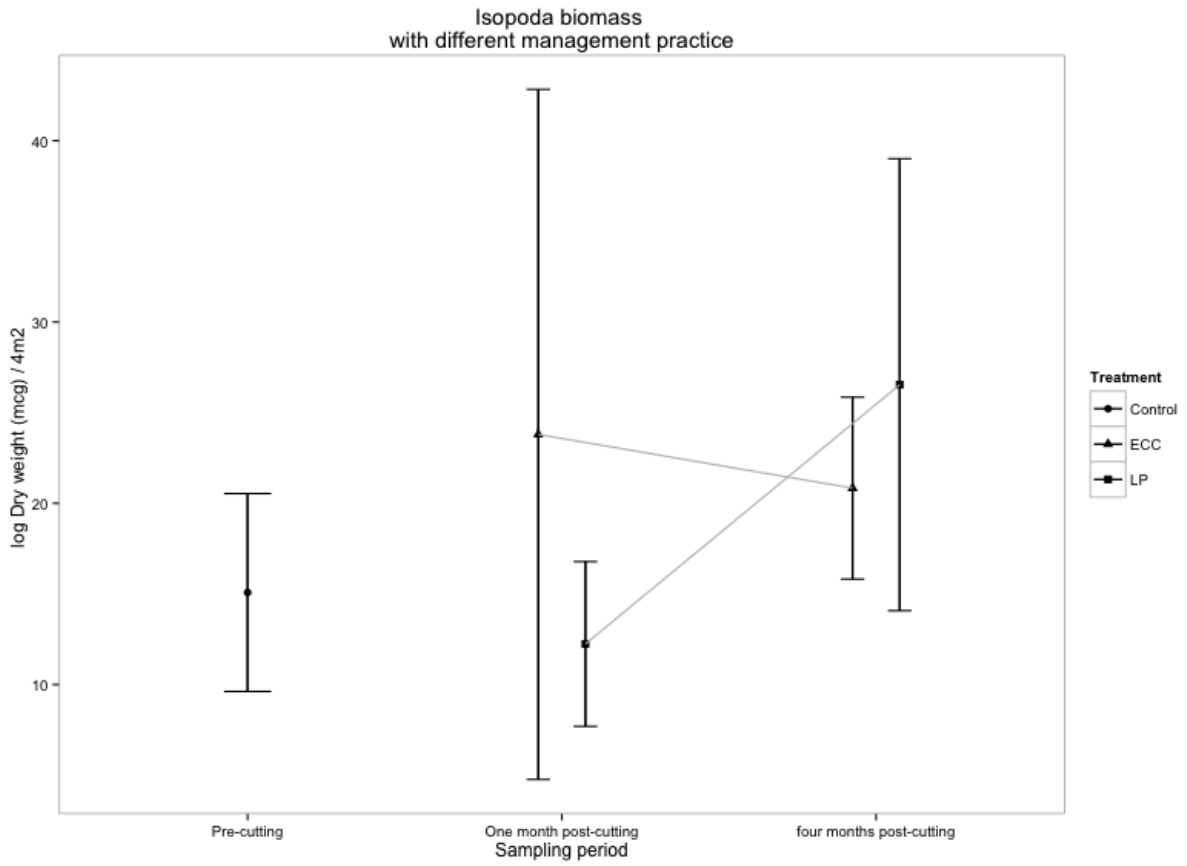


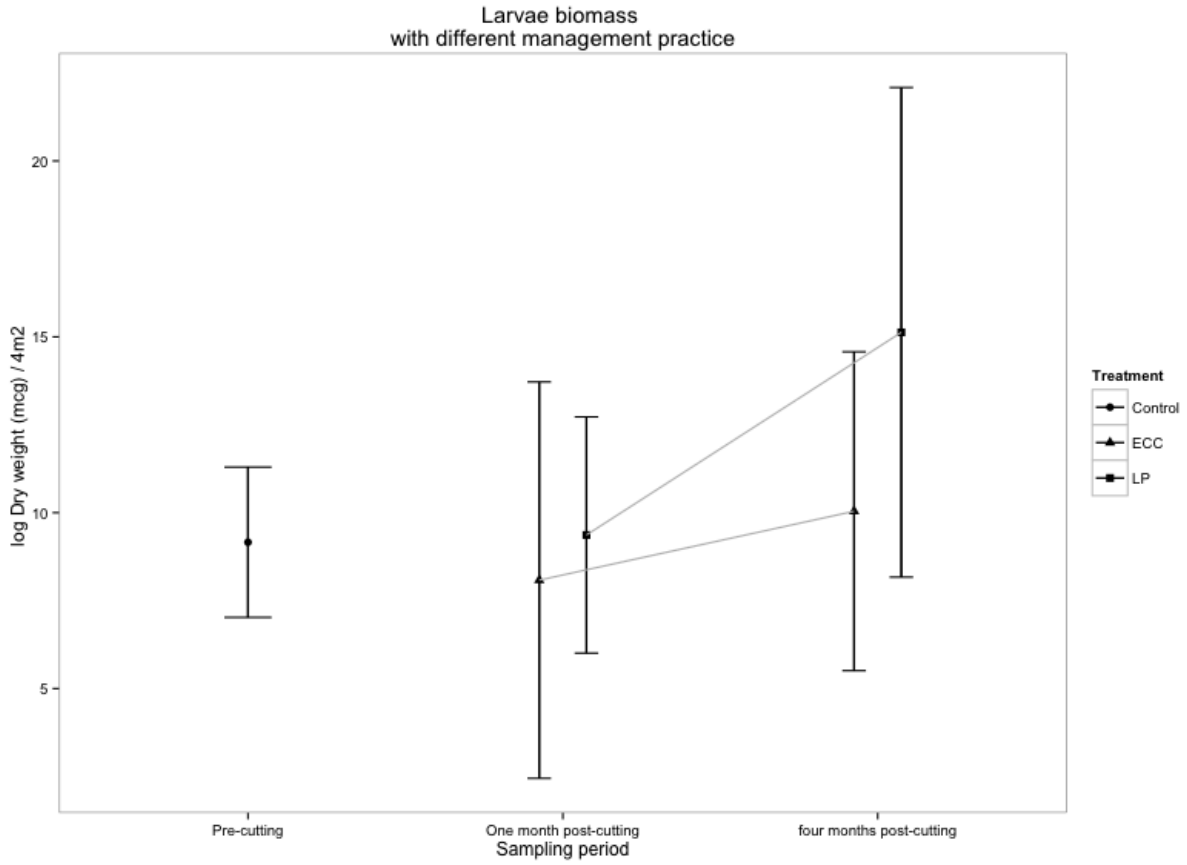
APPENDIX 5: Invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over study period. Error bars represents ± S.E.



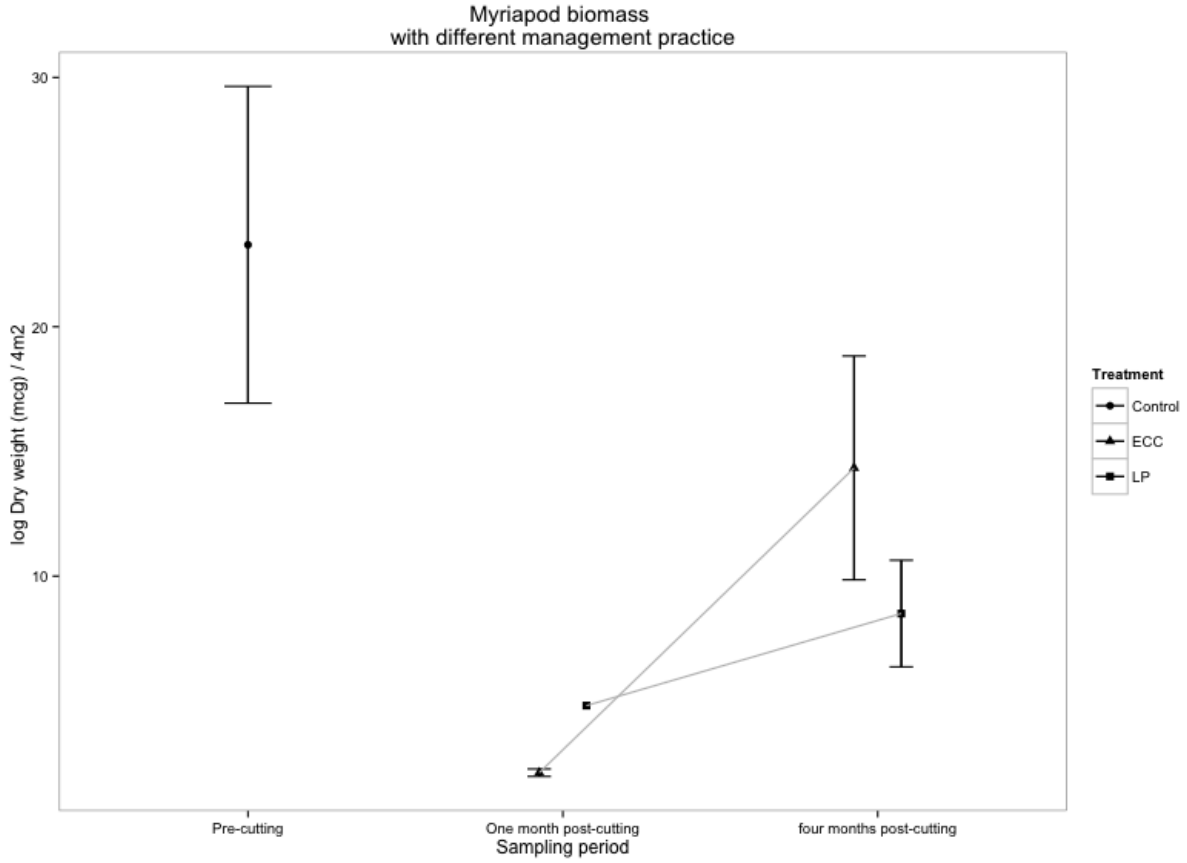


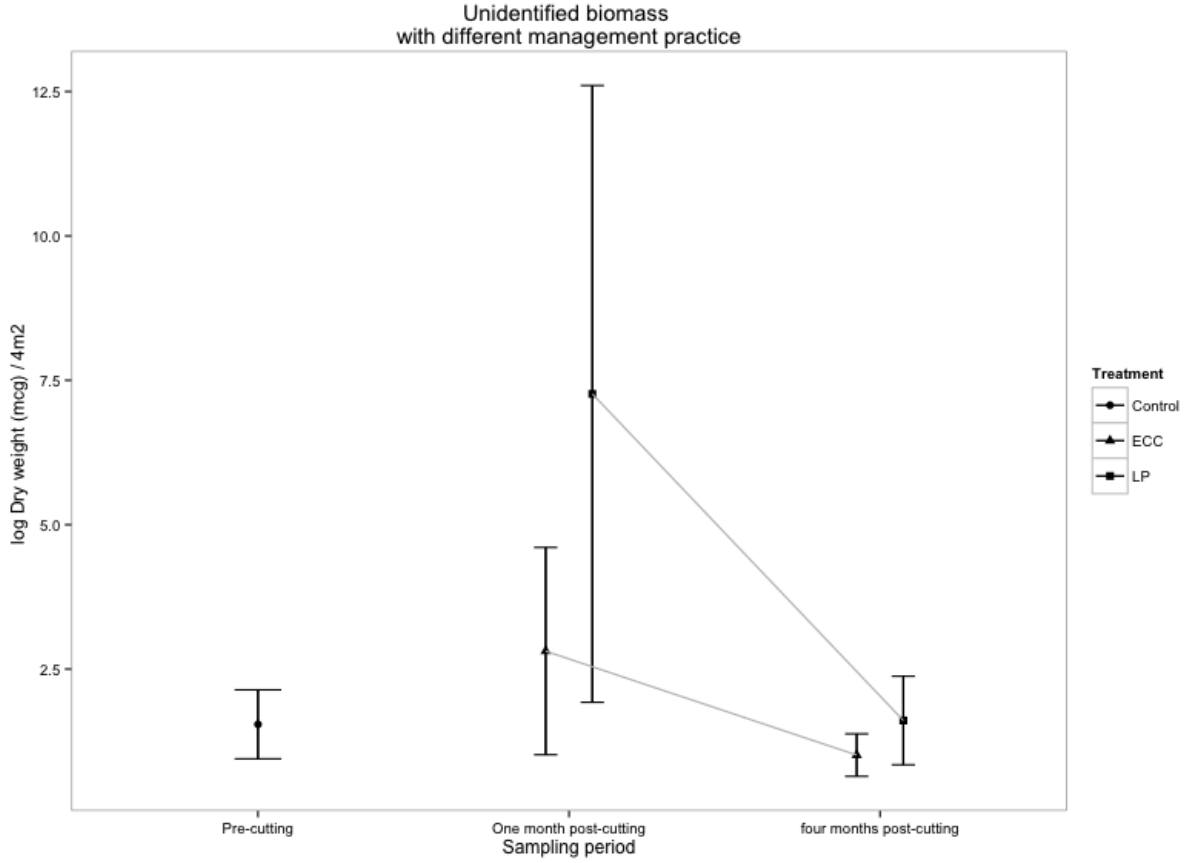
APPENDIX 6: Invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over study period. Error bars represents ± S.E.





APPENDIX 7: Invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over study period. Error bars represents ± S.E.





APPENDIX 8: Effects of climber-cutting on invertebrate biomass not effected by climber-cutting (μg / 4 m^{-2} /$plot^{-1}$) over sampling period. Error bars represents ± S.E.

Chapter 5: **General discussion**

General discussion

Throughout South-east Asia, a large majority of lowland tropical forests have undergone at least two cycles of selective logging. Depending on the intensity of the logging operations, these forests often remain in a state which natural regeneration of the climax tree species has been often disrupted by faster growing pioneer species and with increasing abundance of woody climbers such as lianas and climbing bamboo. In this thesis, We examine the effects of two major restoration practices (line planting and enhanced climber-cutting) that are currently being carried out in order to assess the effects on forest dynamics, future tree species composition, biomass gain, and arthropod diversity.

Litter and canopy dynamics

In chapter two, we found that the increase in intensive management of woody climbers (lianas and climbing bamboo)with the enhanced climber-cutting treatment (ECC) had increased litter fall by 130% relatively fast. This increased took place between 56 to 112 collection days. The increase however did not remain high. the short term increase returned to baseline levels (Line planting method used as a control) between collection day 130 to 140 (74 to 84 days after treatment). Over the period of one year, we found the treatment increased litter fall production by 17% more then the standard line planting method. With this, we found that the enhanced climber-cutting treatment was shown to increase light conditions to the forest floor by 47% (on average 4.9% to 7.2% full sunlight).

Lianas and climbing bamboo play an important role in litter production, and provide important ecosystem services such as the contribution to forest substrate and the cycling of nutrients. We hypothesized that the eradication of climbers may lead to an overall decrease to the production of litter by 20% based on findings by Phillips (2008) who investigated roles of lianas in tropical forests. However this was not found in this study, after the initial pulse of litter cause by the death of the climbers, the overall litter levels returned to baseline levels and remained constant to the line planting method. We however found that this treatment negatively impacted the production of fruits and flowers, reducing the production of reproductive parts by

81%. This reduction may negatively impact food supplies for a range of fauna that are depended on frequent flowering and fruit production of lianas.

Growth and mortality of planted seedlings

In chapter two, we investigated the effects of the climber-cutting method on enrichment planted forests. We planted and monitored 2107 dipterocarp seedlings and subjected the seedlings to two forest management treatments: the line planting and enhanced climber-cutting silvicultral treatments. Sixteen species of lowland dipterocarp seedlings were monitored over a 2.6 year period (953 days) and multiple growth measurements were carried out. On average, we found that the climber-cutting treatment increased basal diameter SGR by 27.79%. The largest difference in basal diameter SGR was seen in *Shorea beccariana*, that grew 88% higher in the enhanced climber-cutting treatment compared to the line planting method. Out of the 16 species studied, we found one species to have performed better in the line planting method (*Parashorea malaanonan*), that grew 14% higher in this treatment.

Overall all species with the exception of one performed positively (increase in growth rates). Rank performance of the species shows that there are some shifts in performance of seedlings between the different experimental treatments (chapter 3) suggesting among these species a preference for a particular treatment. We found at both extremes of the ranks, seedlings maintained their performance level (+/- one rank) however, intermediate ranked seedlings showed a larger difference in performance ranking. Eight species increased in rank performance in the enhanced climber-cutting treatment with a further seven species decreasing in ranks. We found no difference in mortality rates between different treatments. This could be because on average, the treatment increased light levels within a range that did not subject these species to extreme stress (from 4.9% to 7.2% full sunlight) thus illustrating that we do not effect planted seedlings negatively.

Our findings show evidence that with intensification of management practices such as the shift from line planting to the enhanced climber-cutting treatment, can improve overall performance of all species. A detailed look at the performance rank shifts suggest that some species outperforms others. This finding

shows that both management strategies will put a range of species in a competitive advantage in terms of growth. We show that at the seedling stage, this treatment highlights that the use of this method on a landscape scale might have future negative outcomes for species composition. Future studies should incorporate more extreme environments in order to determine clear responses of seedlings to different treatments and correlate these findings with simple traits that can be accessed in field conditions. With this findings, we can improve recommendations to forest managers by providing simple keys to be able to predict performance of seedlings based on their morphological traits in order to increase performance of seedling without effecting future species composition of these managed forests.

Arthropod biomass dynamics

In chapter four, we investigated how the two different treatments effected communities of canopy arthropods. We sampled sites prior and post climber-cutting treatment implementation and resurveyed sites by insecticide fogging one and four months post treatment. Out of the 20 sampled ordinal groups we found four groups to be effected by the treatment. The groups that were effected included Blattodea (roaches), Hymenoptera - family: formicidae (ants), Hemiptera (bugs) and Coleoptera (beetles). Out of these four groups effected, Blattodea (roaches) showed an increase in biomass by 388% and Hymenoptera - family: formicidae (ants), decreased by 45% in biomass when compared to pre-cutting (control) samples. These two groups did not return to control biomass levels four months after the treatment had ben implemented. Hemiptera (bugs) and Coleoptera (beetles) biomass increased by 31% and 59% respectively one month after treatment however, returned to control levels four months after treatment had been implemented.

Our results show that the ordinal groups that were primarily effected were those which were most abundant and that was directly effected by the changes the enhanced climber cutting treatment is responsible for. Roaches showed the largest increase in biomass and was caused primarily by the increase availability of their food supply. A large amount of species within the roach order feed on forest floor detritus which in chapter two we saw increase rapidly, this increase in litter and decaying wood primarily caused roach biomass to increase (Adl 2003). Ants have often been found to use climbing plants such as lianas and bamboo as nest sites (Buschinger et al. 1994). With up to 28 species of ants and 10 species of hemipterans found being

associated with climbing bamboo (Blüthgen et al. 2006), we found that the treatment decreased ant biomass because of the disruption of their habitat space. We found that the Hemiptera order increased in the short term. This increase could have been caused by the sudden increase in new leaf production which often takes place when light levels increase. Borghesio (2012), studying gap creation in old growth forest found that Hemiptera abundance increased with increased amount of disturbance similar to what we have found.

Implications for forest restoration

Conclusions that can be made from this overall study can imply that the enhanced climber-cutting treatment overall, does not place our studied dipterocarp species in a disadvantage. From chapter three we see that all species showed an increased in growth rate in the enhanced climber-cutting treatment with an exception for one species that showed a weak preference towards the more conservative line planting method. The treatment does not effect mortality of the studied species as the treatment on average, increases light levels moderately to a level that these species can tolerate.

Major negative implications of the treatment include the increase of litter fall rates by 130%. This increase in litter volume will need to be considered in restoration programs aiming to use the climber cutting treatment for increasing carbon gains. The climber-cutting treatment was seen to decrease plant reproductive parts (flowers and fruits) by 81% when compared with the line planting method. This large decrease in fruit and flower production may have a high negative impact on local fauna and will have to be assess in greater when used along side reforestation programs aiming to increase biodiversity values of logged over forests. Finally, in chapter four, we show that the treatment showed little to no effect on arthropod biomass. Four ordinal groups out of the 20 that was sampled were seen to be effected by this treatment. Out of those that were effected two returned to baseline levels, and a further two (roaches and ants) remained effected four months after treatment. Longer term studies looking into the the effects of this treatment on roaches and ants are required in order to understand the effect of this treatment on these orders.

Future research

Like many experimental studies, this research has highlighted gaps in our understanding of tropical forest ecology and restoration which has raised concerns which were outside our study scope. In chapter two we show how the climber-cutting treatment opens the canopy and increases litter fall volumes. This opening of the canopy may change the forest floor conditions by drying, and concerns on how this alters the litter microhabitat has arose. A study by Saner *et al*. (2009) found that forest gaps in both logged and primary forest exhibited a reduced rate of soil respiration caused by an increase in soil temperature, a decrease in litter fall and fine root biomass. The small opening of the canopy in our study coupled by the increased in litter fall may cause some changes in the dynamics of soil respiration that has yet to be investigated. An insight into this concern has been highlighted by a study carried out by Sayer et al. (2007) that found that adding litter to the forest floor increased soil respiration by 40%. This increase was caused by the stimulation of the decomposition of older soil organic matter by the addition of fresh organic matter (Sayer et al. 2007). This large change in soil respiration can lead to an increased in carbon output which may in-turn be an important factor for restoration projects that use the climber-cutting treatment as a method to increase carbon gains. In chapter two, we exhibit an understanding on how much volume of fine litter was produced by the climber cutting treatment, however we encountered difficulties in capturing its affects on larger debris such as large lianas. More intense sampling methods to include large lianas will have to be developed in order to estimate the volume of dead biomass produced when carrying out such treatments. Estimates from this will give us a more accurate understanding on how much biomass is loss during the early stages of this treatment.

A major aim of this thesis was to provide a holistic understanding of the climber-cutting treatment and its effects on lowland dipterocarp forests regeneration. Future avenues for the expansion of this research can be in the direction of creating a key that can be useful for forest managers. In chapter three we found some weak correlations between how different species respond to the treatments and how it is correlated to some key functional traits. The forest conditions in our field experiments did not highlight a strong difference between different seedlings, however the weak signals illustrate that species functional traits can be used as a predictor of how species respond to the climber cutting treatment. A recent study carried out by Ruger *et al*. (2012) illustrates that several key functional traits can be used as a predictor of how species can respond to

increased resource availability (for example an increase in light conditions). Ruger *et al*. (2012) found wood density remained one the most determinant factor indicating that species with low wood densities were able to respond quicker during periods of hight light availability, however these species showed a decline in growth rates at larger size when compared to species with dense wood that showed increasingly faster diameter growth at larger sizes. Simplistic correlations with growth rates as illustrated here can be used in providing forest managers with an understanding when (at which size class) and where (composition of seedlings) should the climber cutting treatment be implemented on to save on costs and to maximise potential output of the silvicultral practice. The maximal height of a species can also play an important role as a trait that forest managers could use. Poorter *et al*.(2008) found that taller statured species grew faster as compared to smaller statured species. Species with taller maximal height were able to respond faster to higher light, suggesting that this characteristics would benefit these species when they are exposed in the upper canopy (Rüger et al. 2012).

In chapter two we found that overall fruit and flower (reproductive organs) production was greatly reduced. How this affects species that are dependent on these fruiting lianas remains to be a question that has yet to be concluded. Not only are climbing plants important food supply for primates (Marshall et al. 2009), they are also an important structure for a range of canopy arthropods (Cleary et al. 2009). Detailed food web interactionsbetween fruiting lianas and fauna that are dependent on them remains an area which would need greater attention in the future in order to asses their contribution to forest food dynamics. The final area of concern lies within the management aspect of the climber cutting treatment.

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Appendix

As part of my thesis, I compiled collaborative work that I have been involved with during my duration of my project. Here I provide a short description of the appendix section of this thesis and the various publications that I have been affiliated with.

Attached as appendix 1 is a paper published in 2011 in the special issue of Philosophical Transactions of the Royal Society B: Biological Sciences: Theme issue 'The future of South East Asian rainforests in a changing landscape and climate'. My contributions to this paper included the creation of the tables and figures and I assisted field measurements contributing to the larger Sabah Biodiversity Experiments including the replanting of seedlings that took place.

In appendix 2, I attach a paper that is currently in review in Ecology and Evolution titled: A Trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific RGRs. Here I contributed by carrying out the re-measurement of seedlings during my Masters and included data imputing and management.

Finally In appendix 3, I include an essay to be published in a coffee table book titled Pusaka Akar. Which covers various aspects of the environmental issues and solutions surrounding Malaysia.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B

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Research

The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning

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Relatively, little is known about the relationship between biodiversity and ecosystem functioning in forests, especially in the tropics. We describe the Sabah Biodiversity Experiment: a large-scale, long-term field study on the island of Borneo. The project aims at understanding the relationship between tree species diversity and the functioning of lowland dipterocarp rainforest during restoration following selective logging. The experiment is planned to run for several decades (from seed to adult tree), so here we focus on introducing the project and its experimental design and on assessing initial conditions and the potential for restoration of the structure and functioning of the study system, the Malua Forest Reserve. We estimate residual impacts 22 years after selective logging by comparison with an appropriate neighbouring area of primary forest in Danum Valley of similar conditions. There was no difference in the alpha or beta species diversity of transect plots in the two forest types, probably owing to the selective nature of the logging and potential effects of competitive release. However, despite equal total stem density, forest structure differed as expected with a deficit of large trees and a surfeit of saplings in selectively logged areas. These impacts on structure have the potential to influence ecosystem functioning. In particular, above-ground biomass and carbon pools in selectively logged areas were only 60 per cent of those in the primary forest even after 22 years of recovery. Our results establish the initial conditions for the Sabah Biodiversity Experiment and confirm the potential to accelerate restoration by using enrichment planting of dipterocarps to overcome recruitment limitation. What role dipterocarp diversity plays in restoration only will become clear with long-term results.

Keywords: enrichment planting; species richness; ecosystem functioning; selectively logged forest; Dipterocarpaceae; Sabah Biodiversity Experiment

1. INTRODUCTION

> 'We have done the easy stuff, working experimentally with herbaceous communities, and have learned a great deal about the diversity/functioning/stability relationship. However, we now must move on to address those ecosystems that control a good portion of the carbon, nutrient and water balances of the earth—the forests'.
> Harold Mooney [1, p. VI]

(a) *Biodiversity and the functioning and stability of ecosystems*

As well as being renowned for their biodiversity, tropical forests also provide multiple local, regional and global ecosystem services [2]. For example, at the global scale, they contribute to climate regulation, whereas at the regional scale they provide water-storage capacity and at the local scale they can support

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One contribution of 16 to a Theme Issue 'The future of South East Asian rainforests in a changing landscape and climate'.

pest regulation, pollination, seed dispersal and soil fertility [3]. However, both the biodiversity and functioning of tropical forest ecosystems are under threat from human activities including over-harvesting of selectively logged trees and forest habitat fragmentation through conversion to agriculture and other land-use changes.

Recent research [4–6] has established that loss of biodiversity can have negative impacts on the functioning and stability of ecosystems. Indeed, Darwin laid out the rationale for a link between biodiversity and ecosystem functioning during the formative years of evolution and ecology [7,8]. Darwin's *principle of divergence* proposed that the evolution of species into different, complementary niches leads to an ecological 'division of labour', such that an ecosystem with a diverse community of species functions more effectively in terms of resource capture and cycling, and higher levels of productivity [9]. Consequently, sudden loss of biodiversity can have a negative effect on functioning by leaving niches vacant or under-used [10].

Meta-analysis has shown that, all else being equal, more diverse communities do indeed lead to more complete resource capture and retention and to higher levels of productivity [4,11–13]. Because different sets of species influence different ecosystem processes, higher levels of biodiversity are required to support full ecosystem multi-functionality than to underpin any single process [14–16]. Diversity also increases stability whenever species in a mixed community differ in their response to perturbation and when diversity increases mean levels of an ecosystem process relative to the variability in that process [17,18]. Ecosystem functioning refers to all the transfers of energy and matter owing to biogeochemical processes (or ecosystem processes) even though (for practical reasons) much research to date has focused on biomass production.

(b) *Does biodiversity loss impact ecosystem functioning in tropical forests?*

Relatively little is known about the relationship between biodiversity and ecosystem functioning in forests, particularly in the tropics. Indeed, one of the most significant recent conceptual advances in tropical forest ecology (and in community ecology in general), the unified neutral theory of biodiversity and biogeography [19], appears to imply no link between diversity and functioning. In neutral theory, species are identical in terms of the small number of traits that play a role in community dynamics, namely birth and death rates and immigration and speciation rates. Species are therefore identical and interchangeable and populations follow the random walk of ecological drift. Because species are identical, they co-occur entirely owing to the so-called equalizing forces that slow time to extinction while density- or frequency-dependent stabilizing forces are absent [20]. The neutral theory is supported by its unexpected early success in recreating realistic community characteristics such as relative abundance distributions. Despite this success, the plausibility of key assumptions of the neutral theory has come under increasing question [21,22]. The debate has now moved on to the relative strength of equalizing and stabilizing in ecological communities, with tropical forests as one system suggested to have relatively strong equalizing forces (species fitnesses are similar) and weak stabilizing forces. If this were the case, then it would appear to suggest only weak effects of biodiversity loss on functioning in forest ecosystems. On the other hand, simulation studies predict impacts of species loss on carbon storage under some extinction scenarios [23].

Most of the evidence for the relationship between diversity and ecosystem functioning comes from observational surveys in temperate and boreal forests [24–26], where it is difficult to separate the effects of diversity from other confounding environmental variables. For example, these natural gradients of diversity often include one species that is present along the entire gradient, confounding species diversity with species identity [24]. Inventory data suggest a positive [27,28] or null [29] relationship between tree diversity and biomass production. Tree diversity has been found to positively affect soil cation exchange capacity [30] and nutrient turnover [31], but also decomposer fauna at the local scale [32]. Forest soil communities show contrasting behaviour in the way species richness and overall density respond to tree diversity: true bugs (Hemiptera, Heteroptera) were primarily affected by tree diversity and heterogeneity [33,34] but herbivores [35] and predatory arthropods [36] were correlated more with tree species identity than with species richness.

Some studies in tropical forests have compared the functionality of monocultures and mixtures in plantations [37,38] with results showing that mixed species stands can sometimes outperform monocultures, but that whether or not this occurs depends on having complementary mixtures of species and not just species richness '*per se*'. Some species grew better [39] and had greater canopy development [40] in mixtures, others in monocultures. Overall, a review of monoculture and polyculture plantations found that mixed species stands tend to be more productive [41]. Apart from these reviews comparing mixed- and single-species plantations, the small literature chiefly comprises work from the Neotropics by Ewel and co-worker [42,43] on predicting complementary mixtures of species and a pioneering biodiversity experiment by Potvin and co-workers [44–46].

The work by Ewel & co-worker involved only three species that were very different from one another. Their results emphasize the importance of species identity (traits) and community composition (interactions in mixture). Species mixtures were sometimes complementary but the balance with competitive interactions changed over time primarily driven by competition for light. Predicting the development of subsequent interactions from the initial combination of species' traits in a community was highlighted as the major challenge for designing utilitarian combinations of species, for use in agro-forestry for example.

In their biodiversity experiment in Panama, Potvin & co-workers planted six tree species in monocultures and mixtures, replicated over 24 plots. The first outcomes indicate a positive effect of biodiversity on productivity

owing to increased individual growth, but without any significant change in mortality rates [44,45]. Tree species richness was found to positively affect soil respiration [47], nutrient storage [48], and nitrogen and phosphorus pools [49], a result mainly explained by complementarity. Litter production and decomposition were primarily affected by species identity [50], although the lack of consideration for spatio-temporal heterogeneity might have influenced this finding.

Most recently, Ruiz-Jaen & Potvin [46] estimated above-ground carbon stocks in 124 subplots of 20 × 20 m of a 5 ha inventory plot in a 200 year-old tropical forest in Panama and used redundancy analysis to compare the influence of (i) tropical plant diversity (four functional groups given by the combinations of trees versus palms and understory versus canopy), (ii) the effects of five abiotic environmental parameters (topography and soil depth, bulk density, texture and colour), and (iii) spatial heterogeneity. Altogether, the three sources of variation accounted for 41 per cent of the variability in carbon storage, with plant functional group diversity accounting for the largest share of the variation at 20 per cent. The environmental variables and spatial heterogeneity, plus their two- and three-way interactions, accounted for the other half of the explained variation. These effects of biodiversity in a 200 year-old forest differ somewhat from those of the approximately 50 km apart plantation experiment described above and they also differ from the finding from the Barro Colorado Island 50 ha plot that there was no relationship between diversity and above-ground biomass [51]. The reasons for the differences in the results from these three studies all based in Panama are not clear but could include differences in the age of forests, rainfall or physical conditions.

(c) *A new biodiversity experiment in the forests of Borneo*

The Sabah Biodiversity Experiment (www.sabahbiodiversityexperiment.net) is part of an informal network of tree diversity experiments (www.TreeDivNet.ugent.be) including the BIOTREE (www.biotree.bgc-jena.mpg.de/deutsch/index.html) and BEF China (www.bef-china.de), where it is currently one of only two tropical studies and the sole study based in the palaeotropics [25]. The experiment differs in some important ways from any other biodiversity experiment conducted to date. Before introducing the experimental design and methodology, we highlight some of these key features. The Sabah Biodiversity Experiment is situated in mixed dipterocarp forest of South East Asia, which differs from those in Africa and Central America by being strongly dominated by a single family of trees, the Dipterocarpaceae [52]. Dipterocarp forests also often have higher canopies and higher above-ground biomass compared with the forests in other parts of the tropics [53]. The experiment is an attempt to transfer ideas and methods developed with model systems to a real-world setting. In particular, selectively logged forests in Sabah and the region are restored using enrichment planting. Enrichment planting is used for a number of reasons in different projects including timber production (e.g. the INNOPRISE corporation), carbon storage (e.g. the INFAPRO project), and the restoration of biodiversity and the forest ecosystem structure (INIKEA). Enrichment planting in Sabah is usually performed by planting seedlings of dipterocarps (and a small number of other species) along cleared lines cut into the selectively logged forest vegetation. So, the aspect of diversity that is manipulated in the Sabah Biodiversity Experiment is that of the enrichment-planted seedlings, and these are placed into an existing matrix of vegetation left over from selective logging.

We introduce the Sabah Biodiversity Experiment in detail and present some initial results. As results will take time to emerge, we focus on documenting the initial conditions and the potential for forest restoration. While alpha and beta diversities of plant species in the selectively logged forest are not reduced, we document the expected changes in forest structure including a reduction of large trees and an increase in saplings. These changes in structure are associated with lower above-ground biomass and carbon stores.

2. METHODS

(a) *Location*

The Sabah Biodiversity Experiment is named after the Malaysian state that forms the northeastern tip of the island of Borneo (figure 1*a*). The region is relatively aseasonal with an annual rainfall of greater than 3000 mm. In 2000, a suitable experimental location was identified in the southern part of the Malua Forest Reserve (05°05′20″ N, 117°38′32″ E, 102 m a.s.l.)—a 35 000 ha area of selectively logged production forest (figure 1*a* inset). The Sabah Biodiversity Experiment Malua field camp is a satellite of the larger Danum Valley Field Centre that lies to the south (22.6 km air distance). The Malua Forest Reserve is part of a concession of 1 million ha that belongs to the publicly owned Yayasan Sabah (Sabah Foundation), whose purpose is to increase the welfare of the local people of Sabah by exploiting common natural resources, primarily timber [54]. Most of the area has been logged twice, once in the 1980s and once within the last 10 years, but an area of unlogged primary forest—the Danum Valley Conservation Area—was left at the heart of the concession. More specifically, the Malua Forest Reserve as a whole was selectively logged during the early 1980s and the area where the Sabah Biodiversity Experiment is now sited between 1984 and 1986. The area was re-logged in 2007 with the exception of the area used for the Sabah Biodiversity Experiment. The pre-logging timber volume was estimated as 193–221 $m^3\,ha^{-1}$ with dipterocarps comprising between 180 and 216 $m^3\,ha^{-1}$. These values are comparable with estimates of above-ground tree biomass at Danum Valley, supporting the comparability of the two sites (Yayasan Sabah, unpublished data; see §4). The soil of the area was classified as orthic acrisol, which is moderately acid (pH < 6), highly weathered and low in available nutrients, with a base saturation of 81 per cent (detailed protocols in the study of Majalap & Chu [55]). It has a marked increase of clay content with depth [56] and a low organic carbon content (topsoil: 1.2%, 1 m depth: 0.6% [57]). Bedrock consists of a mixture of mudstone and sandstone areas with other

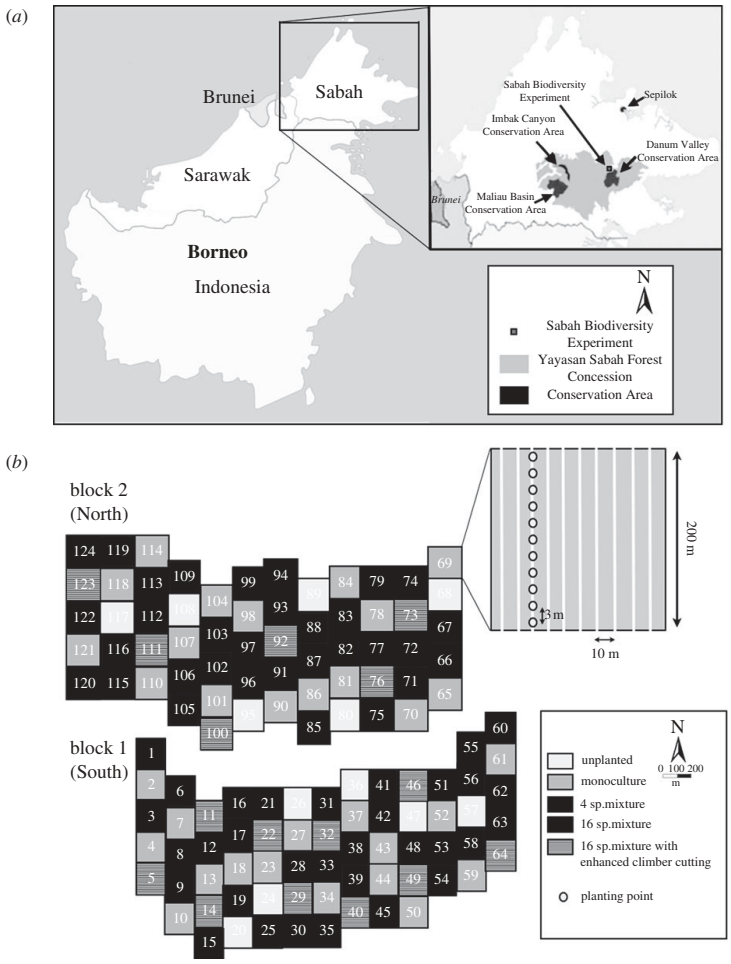

Figure 1. (*a*) Location of the Sabah Biodiversity Experiment within Borneo, Sabah and the local area (inset) showing some of the major areas of conserved forest. (*b*) Plan of the experimental site and enrichment-planting lines (inset).

miscellaneous rock types (Sabah Forestry Department 2010, unpublished data).

The most recent development relevant to the Sabah Biodiversity Experiment and the Malua Forest Reserve is the creation in 2008 of the Malua BioBank (www.maluabank.com), comprising 34 000 ha under a Conservation Management Plan that aims to 'improve wildlife habitat and promote ecosystem service functions including carbon sequestration and storage in above-ground biomass' in order to sell Biodiversity Conservation Certificates representing 100 m^2 of forest. The Sabah Biodiversity Experiment should therefore provide scientific information that could be used to guide and assess the management of the Malua BioBank.

(b) *Experimental design*

The Sabah Biodiversity Experiment is a field scale forest rehabilitation project and tree biodiversity experiment that covers 500 ha. Seedlings of 16 native canopy tree species (Dipterocarpaceae; table 1) were enrichment planted along lines cut into the pre-existing selectively logged forest (figure 1*b*). The project comprises 124 4 ha plots (200 × 200 m) that follow a randomized block design. The core of the project is the set of 96 plots that form a gradient in the species richness of enrichment-planted dipterocarps, which includes enrichment planting with one of each of the 16 study species, 16 different four-species mixtures and all 16 species combined. Each diversity level comprises 32 plots divided equally between the two blocks so that each of the enrichment plantings using one or four species occurs once in each of the two blocks with 16 identical replicates of the full 16-species enrichment-planting mixture in each block. Responses in ecosystems properties and processes along this gradient of 96 plots enrichment planted with one, four or 16 species can be compared with those of 12 unplanted control plots (six in each block). The diversity gradient of 96 plots plus unplanted controls sum

Table 1. The 16 species of the Dipterocarpaceae family planted in the Sabah Biodiversity Experiment and their IUCN Red List status (downloaded on 20 November 2010 from www.iucnredlist.org).

genus	species	species authority	IUCN status
Shorea	*johorensis*	Foxw.	critically endangered
	gibbosa	Brandis.	critically endangered
	argentifolia	Sym.	endangered
	faguetiana	Heim.	endangered
	leprosula	Miq.	endangered
	macrophylla	Ashton	vulnerable
	macroptera	King	—
	ovalis	Korth.	—
	parvifolia	Dyer.	—
	beccariana	Bruck	not listed
Parashorea	*malaanonan*	(Blanco) Merr.	critically endangered
	tomentella	Meijer	not listed
Hopea	*sangal*	Korth.	critically endangered
	ferruginea	Parijs	critically endangered
Dryobalanops	*lanceolata*	Burck	endangered
Dipterocarpus	*conformis*	Slooten	—

to 108 plots divided equally between the two blocks. The final 16 plots form a sub-experiment to look at management treatments involving the frequency with which climbing plants (lianas) are removed during restoration. Standard enrichment-planting methods involve cutting of planting lines and of climbing species that would otherwise compete and damage the dipterocarp seedlings [58]. A recent suggestion to speed-up restoration of selectively logged dipterocarp forest is enhanced climber cutting, where the cutting occurs more widely in the intervening areas separating the planting lines that run in parallel at 10 m intervals. The final 16 plots will receive enhanced climber cutting for comparison with matched 16-species plots from the core diversity gradient. The initial plan was to have two identical blocks but for various logistical reasons (erosion of plots, neighbouring streams, etc.) the two blocks have different numbers of plots with 60 in the Northern block and 64 in the South and the replication of the enhanced climber-cutting plots is therefore unequal with six plots in the Northern block and 10 in the South.

(c) *Planting and replanting*

The seedlings required for the initial planting were collected throughout the neighbouring Ulu Segama and Malua forest reserves with the exception of *Hopea ferruginea* (INIKEA nursery at Lawasong) and *Dipterocarpus conformis* (Tawau Hill area collection). The ages of the seedlings varied but were predominantly from a single fruiting and seedlings were selected to be of as similar size as possible. The planting material was assembled at the Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO) nursery in 2001, with the first round of planting beginning in July 2002 with block one completed by December and block two completed in September 2003. Seedlings are planted on parallel lines 10 m apart with one seedling planted every 3 m (except where not possible due to rocks, streams, etc.). It is standard practice to have one round of replanting following a period to allow initial mortality to occur. Therefore, a second collection of seedlings was assembled at a purpose-built nursery in the Malua field camp from both local fruiting events and the INFAPRO nursery. Replanting began in January 2009, and the first block was completed in October 2010. Final seedling collections in December 2009 and August 2010 provided the final seedling stock for replanting of the second block, which is underway at the time of writing and planned for completion during 2011. The survival and growth of the enrichment-planting seedlings are being regularly monitored.

(d) *Diversity and composition*

Four identical transect plots of 10×250 m were established in the primary forest of Danum Valley Conservation Area and in the Sabah Biodiversity Experiment (surveying only the background vegetation between the planting lines). All trees greater than 10 cm diameter at breast height (d.b.h. at 130 cm) were identified by a local tree expert to genus level, or to species level where possible. In 1 ha, we identified 104 species in unlogged forest of Danum Valley and 107 species in selectively logged forest of the Sabah Biodiversity Experiment (electronic supplementary material, table S1). For comparison, an independent survey of the same area of selectively logged forest identified up to 180 species for a total area of 5.25 ha (Sabah Forestry Department 2010, unpublished data). Further details are available in the study of Saner [57]. Forest community composition was analysed with non-metric multidimensional scaling (NMDS) ordination to identify the effects of disturbance history on plant community assemblage. The proportion of each species in a transect plot and the Bray–Curtis dissimilarity function were used to calculate the distance matrix [59]. Alpha and beta diversities were calculated with Shannon's diversity index and Whittacker's measure of beta diversity, respectively [60]. This was implemented using the diversity function in the vegan package in R [61]. Values were calculated per transect plot within each forest type and means and standard errors were calculated from these values.

(e) *Structure and functioning*

Above-ground tree biomass was calculated for unlogged forest and for selectively logged forest based on d.b.h. measurements. Total stand basal area was calculated from d.b.h. and height and volume were predicted from d.b.h. using established allometric equations from Pinard [62]. Above-ground stem (trunk) biomass for individual trees was then calculated by multiplying volume with wood density. Total above-ground biomass was then calculated by multiplying above-ground stem biomass by the standard factor of 1.9 [63]. Carbon stocks were estimated only for the logged forest

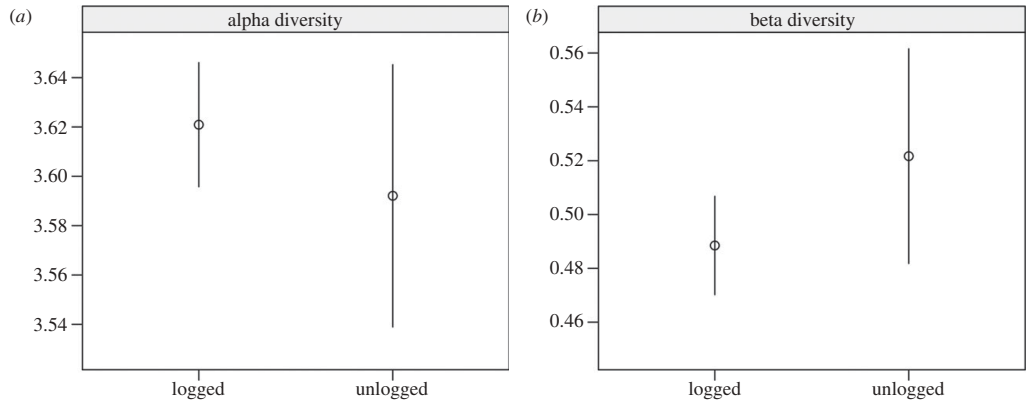

Figure 2. (*a*) Alpha and (*b*) beta diversities in selectively logged and unlogged forests (mean ± s.e.m.; $n = 4$). Shannon's diversity index estimates the number of species per transect lines within each forest type and Whittacker's beta diversity estimates the similarity/turnover in species between transect lines within each forest type.

following the standard assumption that half of above-ground biomass is carbon [63,64].

(f) *Baseline carbon details*

Apart from above-ground tree biomass, several other components of the baseline carbon estimation were estimated or measured along the transect plots of the selectively logged forest. Below-ground coarse roots were estimated from existing root shoot ratios (17% of above-ground tree biomass [65]). Dead standing trees were surveyed and their contribution to total carbon stocks was calculated based on d.b.h. measurements and a mean wood density of 500 kg m^{-3} [66]. Furthermore, litterfall traps (1 m^2, $n = 40$) were randomly allocated along the transect plots, and fine litterfall was collected every other week over one year ($n = 25$). At the same 40 sites, soil respiration rates were estimated using an infrared gas analyser CARBOCAP GMP343 (Vaisala, Finland) and a self-made chamber [67]. Over two months, nine measurements were performed (seven day-time (08.00–12.00) and two night-time (20.00–04.00) measurements) over 5 min intervals. Along the transect plots, quadrats (5×5 m, $n = 24$) were randomly selected and all saplings and seedlings were harvested. Subquadrats (0.5×0.5 m) were established within quadrats for collecting the standing litter, including leaf litter and woody debris. Within each subquadrat, vertical cores (100 cm^3) were taken from the top soil (0–5 cm) to determine fine root biomass (≥2 mm diameter). All collected samples were dried in a glasshouse (7 days, 60°C) prior to measurement. A carbon content of 50 per cent of total biomass was used for harvesting saplings, seedlings and fine root biomass and 42 per cent for fine litter fall, leaf litter and woody debris.

Thirteen random sites were selected across the Sabah Biodiversity Experiment for a soil organic carbon profile down to 1 m depth. Soil pits were excavated and soil cores were taken from layers of 0.1 m depth ($n = 396$). Carbon content was determined by the Walkley–Black method, a wet chemical analysis. For further details on any of these components of the baseline carbon estimation, see Saner [57].

(g) *Species functional traits*

Wood density was estimated with a random intercept linear mixed effects model using all the data on Dipterocarpaceae from www.worldagroforestrycentre.org and Burgess [68]. Site-specific estimates for a subset of species were also made following the water-displacement protocols of Chave *et al.* [69], which correlated strongly with the previously published data (data not shown). Seed volume was estimated using measurements from the literature (calculated as a spheroid based on mean nut length and width estimates obtained from Newman *et al.* [70,71]). Survival, a key demographic process, was estimated for each species as the proportion of the first round of enrichment-planted tree seedlings surviving after seven years. Further details can be found in the study of Dzulkifli [72].

3. RESULTS

(a) *Diversity and composition*

Logging had no effect on average alpha or beta diversities of transect plots within each forest type (figure 2). This was not an effect of differences in individual tree density (see below and tables 2 and 3). However, the NMDS multi-variate analysis suggests that logging had impacts on species composition, with Malua and Danum transect plots clustering on opposing sides of NMDS axis 1 (figure 3). The NMDS shows a large dissimilarity in species composition between unlogged and selectively logged forest transect plots as well as identifying only a handful (<25) of shared species.

(b) *Structure*

Logging had the expected impacts on forest structure, even 22 years after disturbance. The total stand basal area for unlogged forest was 29.9 ± 0.7 versus 25.0 ± 0.8 s.e.m. m^2 ha^{-1} for logged forest (tables 2 and 3). The relative contribution of dipterocarps to total basal area was approximately 60 per cent in unlogged forest when compared with about 30 per cent in logged forest. Trees greater than 90 cm d.b.h. were entirely

Table 2. Unlogged forest: overview of the nine most important tree families and the 10 most important species (>10 cm d.b.h.). BA, mean (±s.e.m.) basal area.

family	species	BA (m^2 ha^{-1})	BA (%)	d.b.h. range (cm)	tree density (ha^{-1})
Dipterocarpaceae		18.24 (±0.66)	61.0	10.1–170.3	87
	Shorea johorensis	9.09 (±0.67)	30.4	10.5–170.3	21
	Shorea parvifolia	6.22 (±0.09)	20.8	11.7–116.3	28
	Parashorea malaanonan	1.61 (±0.26)	5.4	10.6–67.2	12
	Hopea nervosa	0.99 (±0.11)	3.3	10.1–47.5	17
Meliaceae		1.91 (±0.11)	6.4	10.0–32.3	61
	Chisocheton sarawakensis	0.55 (±0.04)	1.8	10.0–30.0	17
	Aglaia elliptica	0.45 (±0.02)	1.5	10.1–31.8	15
	Aglaia macrocarpa	0.39 (±0.03)	1.3	11.4–31.0	10
Leguminosae		1.89 (±0.40)	6.3	10.0–144.8	6
	Koompassia excelsa	1.65 (±0.41)	5.6	144.8	1
Lauraceae		1.33 (±0.09)	4.4	10.0–45.6	44
Euphorbiaceae		1.13 (±0.08)	3.8	20.0–36.1	61
Myrtaceae		0.98 (±0.13)	3.3	10.7–57.1	19
	Syzygium fastigiatum	0.63 (±0.12)	2.1	14.1–57.1	5
Tiliaceae		0.76 (±0.08)	2.5	10.0–43.1	21
	Pentace laxiflora	0.65 (±0.08)	2.2	11.4–43.1	15
Fagaceae		0.62 (±0.06)	2.1	11.7–50.5	10
Burseraceae		0.38 (±0.03)	1.3	10.6–41.4	11
others		2.67 (±0.04)	8.9	10.0–52.0	99
total		29.91 (±0.66)	100	10.0–170.3	410

Table 3. Logged forest: overview of the nine most important tree families and the 10 most important species (>10 cm d.b.h.). BA, mean (± s.e.m.) basal area.

family	species	BA (m^2 ha^{-1})	BA (%)	d.b.h. range (cm)	tree density (ha^{-1})
Dipterocarpaceae		6.88 (±0.17)	27.6	10.0–84.3	69
	Shorea johorensis	1.61 (±0.17)	6.4	13.8–84.3	7
	Shorea gibbosa	1.54 (±0.14)	6.2	10.6–72.5	13
	Dryobalanops lanceolata	0.86 (±0.08)	3.4	12.8–72.1	7
	Shorea fallax	0.67 (±0.17)	2.7	13.4–71.0	3
	Dipterocarpus caudiferus	0.59 (±0.10)	2.4	9.8–60.5	10
Euphorbiaceae		5.42 (±0.24)	21.7	10.0–64.0	107
	Macaranga pearsonii	2.75 (±0.21)	11.0	17.0–64.0	24
	Macaranga gigantea	1.29 (±0.05)	5.2	13.0–38.8	23
Rubiaceae		3.79 (±0.16)	15.2	10.0–48.0	74
	Neolamarckia cadamba	3.11 (±0.13)	12.4	10.2–48.0	33
Leguminosae		0.84 (±0.10)	3.4	10.3–72.8	14
Datiscaceae		0.79 (±0.16)	3.2	23.8–80.9	4
	Octomeles sumatrana	0.79 (±0.16)	3.2	23.8–80.9	4
Lauraceae		0.75 (±0.07)	3.0	11.1–59.8	12
Sonneratiaceae		0.71 (±0.14)	2.8	14.2–77.2	5
	Duabanga moluccana	0.71 (±0.14)	2.8	14.2–77.2	5
Sapindaceae		0.55 (±0.06)	2.2	16.5–51.2	8
Tiliaceae		0.54 (±0.07)	2.2	11.5–62.1	8
others		4.69 (±0.13)	18.8	10.0–59.1	116
total		24.96 (±0.83)	100	10.0–84.3	417

absent from the transects in the logged forest but present in matched transect plots in the primary forest of Danum Valley (figure 4*a*). Differences in total basal area were owing to tree size and not tree density which was similar in the two forest types: the unlogged forest had a total of 410 stems in the surveyed hectare (sum of the four transect plots) versus 417 in the hectare of logged forest. The frequency of the smallest measured trees (10–20 cm) was lower in the logged forest (figure 4*a*).

(c) *Ecosystem functioning: carbon stocks*

Because approximately 65 per cent (155 ± 10.3 s.e.m. Mg ha^{-1}) of the total carbon of tropical lowland dipterocarp forest occurs in above-ground biomass, logging can have large impacts on the carbon stocks of these ecosystems by removing the larger species with denser wood. Estimates from our data of above-ground tree biomass of the selectively logged forest were only 272.1 Mg ha^{-1} (95% CI: 225.6–318.6) compared to 468.6 Mg ha^{-1} (261.6–675.7) in the

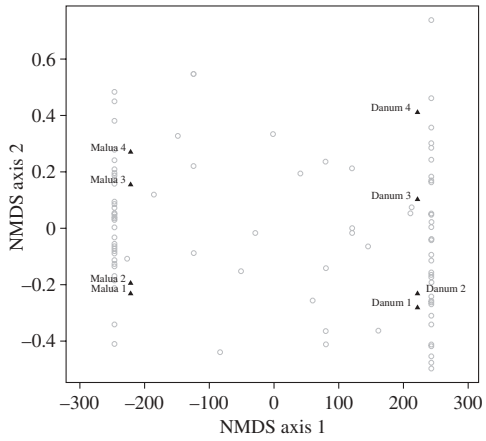

Figure 3. Differences in species composition of transects (solid triangles) and in individual species occurrence (open circles) in the Sabah Biodiversity Experiment area of the selectively logged forest of the Malua Forest Reserve (Malua 1–4) and the primary forest of Danum Valley Conservation Area (Danum 1–4) as shown by the first two axes from a multi-variate NMDS analysis.

primary forest of Danum Valley (figure 4*b*). As around 50 per cent of wood is assumed to be carbon [63], this leads to estimates of carbon stored of 136 Mg C ha^{-1} ($\pm$7.3 s.e.m.) in the selectively logged forest compared with 234.3 Mg C ha^{-1} ($\pm$32.5 s.e.m.) in the primary forest of Danum Valley (figure 5). Based on these estimates, the total area of 500 ha for the Sabah Biodiversity Experiment has an initial pre-enrichment planting total organic carbon content of 118.6 Gg C $\pm$ 4.2 (s.d.).

(**d**) *Species differences*

Preliminary inspection of our data on the traits of dipterocarps suggests substantial species differences. Wood density varies from 440 to 736 kg m^{-3} (figure 6*a*). For context, Borneo Ironwood or Belian (*Eusideroxylon zwageri* Teijsm. & Binnend.) has an air-dry density of 1000–1105 kg m^{-3}, while early successional *Macaranga* species have a wood density ranging from 270 to 590 kg m^{-3} (at 15% moisture content). Seed size also varied widely across three orders of magnitude from 0.028 to 28 cm^{-3}. Finally, survival of the enrichment-planted seedlings had a median value around 40 per cent but varied from approximately 10 to 60% (figure 6*c*).

4. DISCUSSION

Overall, the results of our comparison of the selectively logged lowland dipterocarp forest of the Malua Forest Reserve with the nearby primary forest of Danum Valley support the expectation that logging has chronic impacts on forest composition, structure and functioning, at least for the first 22 years since harvesting.

One exception was that the alpha and beta diversities of the transect plots in the selectively logged forest were not reduced (figure 2) [73]. This was not a function of differences in tree stem and trunk density, which was very similar in the two forest types. Rather, this is probably partly because, by definition, selective logging removes a restricted range of species (here mainly dipterocarps) [74]. Selective logging may also have beneficial effects on the diversity of the pioneers and other non-harvested species through disturbance and release from competition with the large dipterocarp individuals that have been extracted [75]. Multi-variate analysis of the composition of the unlogged and selectively logged forest transect plots supports this explanation with apparent clustering of plots from the two forest types (figure 3), and while pioneer species were present in the selectively logged forest they were not detected in the samples from the unlogged forest.

These differences in composition had both structural and functional consequences 22 years after logging. As expected from its nature, selective logging reduced the frequency of large trees. Indeed, no trees greater than 90 cm d.b.h. were found in transect plots in the selectively logged forests, whereas trees up to twice this diameter were present in the samples from the primary forest of Danum Valley (figure 4*a*). It is important to point out that some larger trees do persist in the selectively logged forest because fewer species were selected for logging in the 1980s than in more recent times (e.g. the legume *Koompassia excelsa* (Becc.) Taub. is sometimes now logged for timber for parquet while previously the silica-rich wood was considered too brittle for any commercial use) and even individuals of desirable species sometimes occurred in inaccessible areas such as on steep slopes. However, it should be noted that the comparisons made here reflect the impact of one instance of selective logging only. Current logging methods include the use of helicopters that enable some of the remaining larger trees in inaccessible spots to be harvested. Comparison of Danum Valley with twice-logged areas of the Malua Forest Reserve would almost certainly reveal larger differences between the two areas and the estimates provided here are conservative in the sense that they consider the effects of only one round of selective logging when most areas have now undergone at least two rounds.

Through the use of bulldozers, dragging of logs on cables, establishment of log landings and so on, logging also damages and kills many seedlings [76] and exert a large impact on rooting and compaction in forest soils [76]. In addition to the reduced number of fruiting mother trees, and subsequent reduction in seedling recruitment, this probably explains the reduced levels of trees with current measurements in the smallest 10–20 cm d.b.h. size class. In contrast, measurements of d.b.h. in the range of approximately 20–80 cm were sometimes slightly above those in unlogged forest, perhaps reflecting reduced competition for seedlings that survived logging and benefited from the removal of larger individuals.

We estimate the total carbon stored in the selectively logged forest to be 237.2 Mg C ha^{-1} ($\pm$8.4 s.d.) with approximately two-thirds above and one-third below ground. The total can be divided into

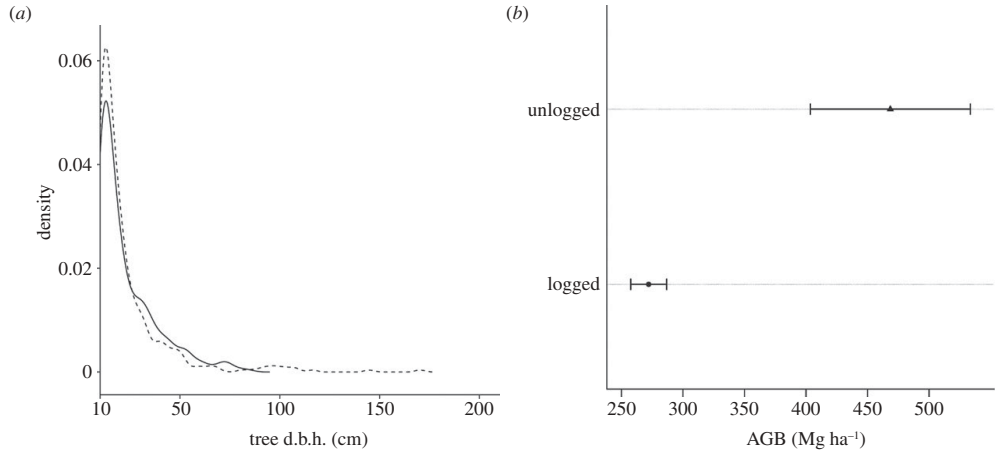

Figure 4. (*a*) Kernel density estimation (probability) of stand size distribution in logged (solid line) and unlogged (dotted line) forests. d.b.h. was measured ≥10 cm only. Note the increased density of mid-sized trees (30–80 cm) in selectively logged forest and the higher density of small (<20 cm) and large (>90 cm) trees in unlogged forests. (*b*) Estimates of total above-ground tree biomass (AGB; ±1 s.e.m.) for the background selectively logged forest of the Sabah Biodiversity Experiment (Malua Forest Reserve) and the primary unlogged forest of Danum Valley.

the following six major carbon pools by percentage (figure 5): above-ground tree (57%) and non-tree biomass (2%), below-ground roots (10%), forest floor litter (<1%), deadwood (6%) and soil (25%). Our results suggest that selective logging of dipterocarps has resulted in the above-ground biomass and carbon pools of the Malua lowland dipterocarp rainforest being depressed by approximately 40 per cent even 22 years after logging. However, indicators of nutrient and carbon turnover rates (dead standing wood, fine roots and litterfall) in the logged forest were not distinguishable from those observed in the neighbouring primary forest of the Danum Valley Conservation Area. This substantial reduction in carbon stocks 22 years after selective logging suggests that restoration and management practices that increase dipterocarp recruitment and basal area in logged dipterocarp forest do have the potential to increase carbon storage during this century by accelerating the return to pre-logging levels [58]. Based on our estimates from the Sabah Biodiversity Experiment (500 ha), enrichment planting in the Malua Forest Reserve (35 000 ha) and in the entire logged concession (1 million ha) has the potential to increase the amount of carbon stored by around 77 t C ha^{-1} in addition to having other potential associated benefits to biodiversity and other ecosystem processes and services. Although we cannot distinguish site from management effects, a survey of unlogged forest at Danum Valley and of the pre-logged forest of the Sabah Biodiversity Experiment completed in 1983 showed that estimated overall volume (unlogged: 178–230 m^3 ha^{-1}, logged: 193–221 m^3 ha^{-1}) and estimated dipterocarp volume (unlogged: 149–225 m^3 ha^{-1}, logged: 180–216 m^3 ha^{-1}) was comparable at both sites before logging in 1986 (Yayasan Sabah Forest Management Plan 1984–2032, unpublished data). We therefore assume that the effect of logging is real and approximately as indicated. For comparison, we also report three studies that independently confirm the effect of logging on approximately 20 years old forest: the study of Berry *et al.* [77] reported a reduction of −99.0 Mg C ha^{-1} (with 95% CI of −162.5 to −35.5), Pinard & Putz [78] −186.5 Mg C ha^{-1} (with 95% CI of −261.7 to −111.3) and Tangki & Chappell [79] −334.7 Mg C ha^{-1} (with 95% CI of −512.4 to −157.0).

Although it is too early to assess the effects of dipterocarp diversity on ecosystem functioning in our experiment, the range of values for the probable functionally relevant traits (figure 6) is consistent with the type of species differences that lead to complementarity [80]. Increasing diversity may therefore be valuable in dipterocarp replanting and restoration schemes [81]. One mechanism by which diversity could enhance forest functioning is a simple spatial insurance effect [17]. Enrichment restoration has traditionally used a small number of species—typically those surviving in nurseries from the last major reproductive event (dipterocarps typically reproduce synchronously and irregularly [82])—and involved planting them in monoculture (or low-diversity combinations) in selectively logged forests. In the long term, this risks enriching forest with a small number of species, setting up a self-reinforcing cycle as these species are over-represented in the next round of reproduction and replanting. So long as no species can survive under all conditions, replanting with one species will result in recruitment failure in unfavourable areas. If density is low enough, this will result in recruitment failure by late-successional species (with higher wood density) and increase the area of forest dominated by pioneer species (with lower wood density). Planting areas with more speciose mixtures with a greater diversity of traits should reduce the risk of this type of recruitment failure

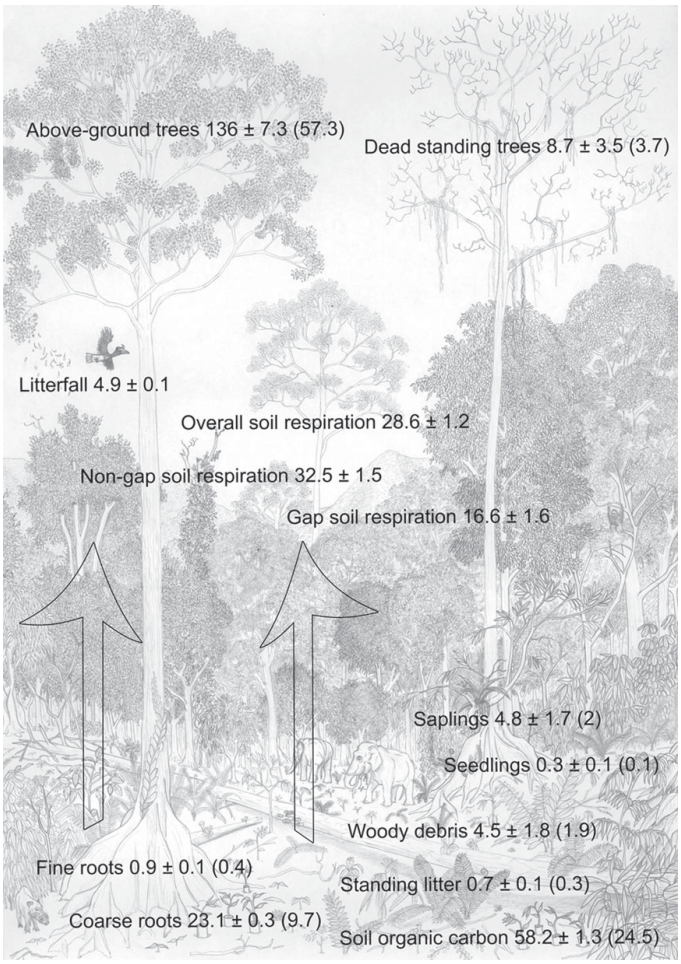

Figure 5. Overview of the baseline carbon budget for the selectively logged forest of the Sabah Biodiversity Experiment. Values are means ± s.e.m. Mg C ha^{-1} (with the per cent contribution to total organic C stocks given in parentheses). Litterfall and soil respiration rates are reported as Mg C ha^{-1} yr^{-1}.

through a spatial insurance effect. Thus, more diverse mixtures should spread risk and increase the chance of having the right species in the right place at the right time.

Selective logging directly and immediately reduces above-ground tree biomass carbon pools in our system by reducing total tree basal area [83,84]. It may have a long-term effect if its selective nature leads to a reduction in average wood density by increasing the abundance of early- relative to late-successional species as discussed above. Restoration and management practices for selectively logged forest that influence recruitment so as to increase total basal area and average wood density therefore have the potential to increase above-ground carbon storage during this century by accelerating the return to pre-logging levels. All else being equal, successful recruitment by species with higher than average wood density will result in greater carbon storage. However, all else may not be equal: enrichment-planting schemes focusing on species with high wood density (presuming a choice including such species is available) could reduce above-ground carbon if wood density trade-offs against other species traits such as growth or recruitment rate. In the long term, enrichment planting could have other feedbacks on forest structure and function via changes in recruitment conditions (light levels, etc.). Understanding the relationship between recruitment, growth rates and relevant functional traits (wood density, etc.) [85] is therefore key to predicting and managing the long-term effects of selective logging and enrichment planting on the structure of the forest and on the services that it provides. Predicting which species provide the most complementary community of species therefore remains a key challenge [43]—especially when multiple forest ecosystem functions are considered. We hope the Sabah Biodiversity Experiment will contribute towards achieving this goal for lowland dipterocarp forests.

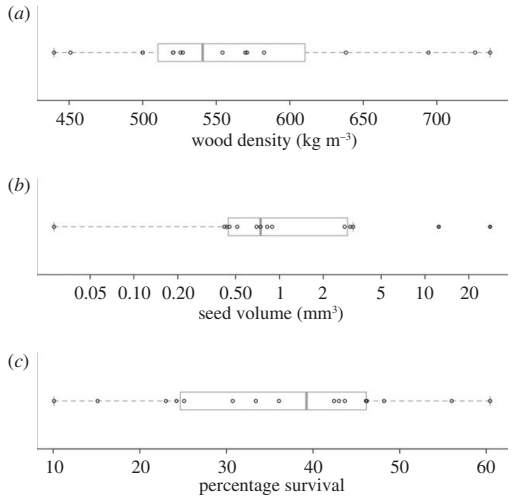

Figure 6. Variation in key functional traits ((*a*) wood density; (*b*) seed volume) and a demographic process ((*c*) percentage survival) of the dipterocarp species used for enrichment planting in the Sabah Biodiversity Experiment. Percentage survival is mean values from the first measure of first planting of the southern block.

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TITLE: A Trait-based trade-off between growth and mortality: evidence from 15 tropical tree species using size-specific RGRs

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RUNNING HEADLINE: Trait-based growth mortality trade-offs

SUMMARY:

1. A life history trade-off between low mortality in the dark and rapid growth in the light is one of the most widely accepted mechanisms underlying plant ecological strategies in tropical forests. Differences in plant functional traits are thought to underlie these distinct ecological strategies, however very few studies have shown significant relationships between functional traits and demographic rates within a functional group.
2. We present eight years of growth and mortality data from saplings of 15 species of Dipterocarpaceae planted into logged-over forest in Malaysian Borneo, and the relationships between these demographic rates and four key functional traits: wood density, specific leaf area (SLA), seed mass and leaf C:N ratio. Species-specific differences in growth rates were separated from seedling size effects by fitting non-linear mixed-effects models, to repeated measurements taken on individuals at multiple time points. Mortality data was analysed using binary logistic regressions in a mixed-effects models framework.
3. Growth increased and mortality decreased with increasing light availability. Species differed in both their growth and mortality rates, yet there was little evidence for a statistical interaction between species and light for either response. There was a positive relationship between growth rate and the predicted probability of mortality regardless of light environment, suggesting that this relationship may be driven by a general trade-off between traits that maximize growth and traits that

minimize mortality, rather than through differential species responses to light.

4. Our results indicate that wood density is an important trait that indicates both the ability of species to grow and resistance to mortality but no other trait was correlated with either growth or mortality. Therefore, the growth mortality trade-off among species of dipterocarp appears to be general in being independent of species crossovers in performance in different light environments.

KEY WORDS:
Dipterocarpaceae; Functional traits; Light; Survival; Non-linear growth; Plant development and life-history traits; SGR; Tropical lowland forest; Wood density

Introduction

Light is generally accepted to be the most limiting resource in tropical rain forests (Whitmore & Brown 1996) and has long been hypothesized to be important in the maintenance of tree species diversity (Denslow 1987). Two mechanisms have been proposed to explain how differences in species-specific responses to light availability may maintain species diversity in tropical forests. First, species that grow well in one light environment have relatively lower growth rates in other light environments (Sack & Grubb 2001; 2003). Second, a trade-off may exist in plant functional traits that result in either low mortality in the shade or rapid growth in high light, but not both (Kitajima & Bolker 2003). However, the relative importance of these two

mechanisms continues to be debated (Baraloto, Goldberg & Bonal 2005; Kitajima & Poorter 2008; Dent & Burslem 2009; Kunstler, Coomes & Canham 2009).

The first mechanism involves partitioning of the habitat with each species performing best (in terms of growth) in a particular light environment. This light partitioning is a result of species responding differently to the light gradient (i.e. a statistical interaction between species and light) and crossing-over in their rank performance as light availability changes. However, there is much debate over whether the magnitude of differential species responses to light is sufficient to generate rank crossovers (Sack & Grubb 2001; Kitajima & Bolker 2003; Sack & Grubb 2003). Many studies present data that illustrate species-light interactions, that result in crossovers in rank performance, and therefore show some support for species specialisation to distinct light environments (Sack & Grubb 2001; 2003; Baltzer & Thomas 2007; Philipson *et al.* 2012). However, there is very limited evidence for a strong trade-off between growth in high- versus growth in the low-light environments, with the general consensus being that this is unlikely to occur (Sack & Grubb 2001; Philipson *et al.* 2012). Furthermore, Kitajima & Bolker (2003) present a detailed analysis showing that crossovers in rank are not statistically supported and rank reversals in performance among light treatments rarely occur. Instead, they argue that low mortality in the shade trades off with rapid growth in high light. This trade-off is a widely accepted mechanism underlying plant ecological strategies in tropical forests (Grubb 1977; Kitajima & Poorter 2008; Wright *et al.* 2010).

Thus, light has been hypothesized to contribute to species coexistence

100 either via species-specific growth responses to a light gradient or via a trade-
101 off between growth in the light and mortality in the shade. These two
102 mechanisms are not necessarily mutually exclusive – species may crossover
103 in growth responses along a light gradient and also species that grow fast in
104 the light, may have increased mortality in the shade. Both mechanisms
105 underpin a gradient in ecological strategy ranging from light-demanding
106 pioneers at one end of the spectrum to highly shade-tolerant canopy trees at
107 the other. Pioneers tend to have high germination rates and maximum growth
108 rates in open disturbed sites, but high mortality in the shade (Swaine &
109 Whitmore 1988). In contrast, shade-tolerant canopy trees tend to have high
110 germination rates and low mortality in deep shade yet their growth rates are
111 constrained. These disparate ecological strategies which govern regeneration
112 dynamics are defined by functional traits and can be illustrated by trade-offs
113 that occur when the functional traits that maximize the fitness of plants in one
114 environment are below-optimal in another environment (Dalling & Burslem
115 2005; Poorter *et al.* 2008).
116 Functional traits such as seed mass, wood density, specific leaf area
117 (SLA) and leaf nutrient concentrations underlie differences in these ecological
118 strategies and are correlated with growth and mortality (Paz & Martinez-
119 Ramos 2003; Ackerly 2003; Poorter & Bongers 2006; Poorter *et al.* 2008;
120 Wright *et al.* 2010). There is substantial evidence that functional traits
121 determine the position of a species along an axis ranging from species that
122 maximise resource-capture and have rapid growth rates at one end of the
123 spectrum to species adapted to resource-conservation and with low mortality
124 at the other end (Kitajima & Poorter 2008; 2010; Wright *et al.* 2010). For

example, it is generally the case that pioneer trees produce large numbers of small seeds, have low wood density and thin, poorly-defended leaves with high nutrient concentrations while shade-tolerant species have the opposite suite of traits; small numbers of large seeds, high wood density etc (Whitmore 1998). However, the relative importance of particular traits, and the relationships among traits and growth and mortality rates, particularly within functional groups - is poorly understood (Larjavaara & Muller-Landau 2010; Wright *et al.* 2010).

These categories of pioneers versus shade-tolerant climax species are established extremes in ecological strategy along the continuum of functional groups (Kariuki *et al.* 2006), and yet within these functional groups there is also high species diversity. Some of the most diverse tropical forests found are on the island of Borneo, where 267 species of trees from the family Dipterocarpaceae dominate the forest canopy (Ashton 1982). Dipterocarps are shade-tolerant canopy trees and represent just one functional group, within which there is a gradient in ecological strategy including a range of mortality and growth rates (Becker, Lye & Goh 1998; Philipson *et al.* 2012). We propose that trade-offs in functional traits may explain the variation in growth and mortality rates and contribute to the maintenance of species diversity within this functional group.

We present eight years of growth and mortality data for 15 species of Dipterocarpaceae saplings planted under heterogeneous canopy cover within an experimental area of selectively logged forest in Malaysian Borneo (The Sabah Biodiversity Experiment; (Hector *et al.* 2011)). We investigate the relationship between mortality growth rates along a light gradient, and

150 determine whether functional traits underpin a trade-off between growth and
151 mortality.
152 Specifically we show:
153 1. There is very limited evidence that species respond differently to variation
154 in light conditions in terms of both growth and mortality rates; all show faster
155 growth rates and declining mortality with increasing light.
156 2. There is a clear trade off between mortality and growth rates in this
157 phylogenetically and functionally constrained group of shade-tolerant trees
158 despite the lack of clear differences in species-specific responses to the light
159 gradient.
160 3. Of the plant functional traits tested, only wood density was correlated with
161 growth and mortality rates.
162

163 **Materials and methods**

164 ***Study Site***

165 The Sabah Biodiversity Experiment (SBE) is located in the Malua Forest
166 Reserve in the eastern region of the Malaysian state of Sabah, Northern
167 Borneo, see Hector *et al.* (2011) for full details. The Malua forest reserve is
168 embedded within the Yayasan Sabah Forest Management Area (YSFMA); a
169 1-million hectare forest concession that includes Danum Valley Conservation
170 Area, extensive areas of forest under management for timber production
171 (approx. 750,000 hectares) and two of SE Asia's largest forest rehabilitation
172 projects (the Sabah Biodiversity Experiment within Malua Forest Reserve,
173 SBE; and the INnoprise - Face foundation Rainforest Rehabilitation PROject,
174 INFAPRO). The region has no distinct seasons with an annual rainfall of

around 3000 mm per year (Saner *et al.* 2011; O'Brien 2013). Temperatures recorded at Danum Valley Field Center (DVFC) were found to be typical of a wet equatorial climate with mean daily temperatures of 26.8°C (Clarke & Walsh 2006).

The seedlings in this study were planted into lowland mixed dipterocarp forest that was logged in the late 1980's. The trees targeted during the logging operation were mostly dipterocarps, which are thus depauperate in the remaining forest. The saplings included in this analysis are part of the SBE forest rehabilitation project, which specifically investigates the effect of altering the diversity of dipterocarp trees by enrichment planting (Hector *et al.* 2011). The INFAPRO enrichment-planting project is one of the most extensive in SE Asia, and the SBE follows the planting techniques of INFAPRO's enrichment planting system as closely as possible, with a view to making the most relevant recommendations for the regions humid forests.

Seedling sources and planting

Seedlings were sourced from INFAPRO. Seeds were collected from the surrounding forest within the YSFMA. Seeds were then stored under wet jute sacks until germination then sown into polyethylene pots (7 x 23 cm) filled with shredded locally collected topsoil. Seedlings were grown under shade-cloth in 10% ambient light and watered twice daily for a minimum of 3 months before being transplanted into the experimental SBE plots (Hector *et al.* 2011). All the saplings included in this study are from six high diversity treatment plots (Hector *et al.* 2011). The average seedling diameter just before planting was 4.12 mm, (range: 2.74 mm - 8.25 mm). The average

number of individuals with more than three size measures required for the growth analysis was 68 (range: 12 -132). Each experimental plot (200 x 200 m) consists of 20 planting lines separated by 10 m. Each 200 m x 2 m planting line was created by manually clearing the understory of seedlings, shrubs, bamboo and lianas. Seedlings were planted every 3 meters along the center of each planting line, unless there was a physical obstruction (river, rocky outcrop etc). Planting was carried out throughout 2002 and 2003. Planting lines were cleared and maintained when required; up to twice annually. The SBE planting methods are described in greater detail in (Hector *et al.* 2011). Six plots to the west of block one, each including all species, were selected for intensive measurements of diameter growth and mortality.

Study species

The species selected for the SBE were restricted to those which a) had sufficient availability at the time of planting in 2002 and 2003, b) were broadly representative of the species composition of the study site, and c) included a range of commonly occurring traits (see Table 1). Fifteen closely related species within the family Dipterocarpaceae were selected. Although all species are shade-tolerant, late-successional canopy trees, they were selected specifically to span the range of shade-tolerance and timber quality within this group: *Shorea johorensis* Foxw., *Shorea gibbosa* Brandis., *Shorea argentifolia* Sym., *Shorea faguetiana* Heim., *Shorea leprosula* Miq., *Shorea macrophylla* Ashton, *Shorea macroptera* King, *Shorea ovalis* Korth., *Shorea parvifolia* Dyer. *Shorea beccariana* Bruck, *Parashorea malaanonan* (Blanco) Merr., *Parashorea tomentella* (Blanco) Merr., *Hopea sangal* Korth.,

Dryobalanops lanceolata Burck, *Dipterocarpus conformis* Slooten. One species present in the SBE experiment, *Hopea ferruginea* Parij, suffered extremely high mortality immediately after planting and before the first data was collected, resulting in insufficient replication for analysis and has therefore been omitted from this study. The abundance and distribution of these species is described in Table 1.

Seedling Measurements

All seedlings were measured and censused for mortality on average 576 days after planting. Seedlings were censused a further six times from 2004 – 2011, after approximately, 815, 1166, 1474, 2885, 3214, and 3214 days after planting. At each census seedling diameter was measured 2 cm from the soil surface and at breast height (1.3 m) if plants were sufficiently tall. Light conditions were assessed at every census using spherical densiometers directly above each seedling (Lemmon 1956). Canopy openness across the study site varied between 0.5% and 25%, representing the full range present in the primary forest. The smallest variation in canopy openness above an individual seedling ranged from 1 – 15% for *S. argentifolia* while the largest variation was 0.5 – 26% for *H. sangal* (Fig. 1).

Trait measurements and estimates

Functional trait data from four experiments conducted at the site were combined to generate a database of leaf and whole plant traits (Philipson 2009; Philipson *et al.* 2012; O'Brien 2013). Linear mixed effects models were used to estimate mean functional traits. Random intercepts were added for

species, experiment and any other design or treatment variables key to any of the datasets. Estimates for the traits where extracted using only the grand mean and species random effects.

Leaf traits

In all four experiments all leaves were collected from all harvested plants, 3285 in total, providing leaves for estimating specific leaf area (SLA). Leaf area was estimated at the time of harvest by photographing all leaves and calculating the area using imageJ software (Abràmoff, Magalhães & Ram 2004). Leaves were then dried at 60° C to constant mass and weighed without petioles. Leaf area and dry mass were used to generate SLA values. The leaves of the final harvest for two experiments (Philipson 2009; Philipson *et al.* 2012) were dried, ground and the total nitrogen was extracted using the Kjeldahl method. Organic carbon was estimated following Walkley and Black (1934).

Whole plant traits

Wood density estimates were generated from the saplings from all three light environments in the shade-house experiment described in Philipson *et al* (2012). These seedlings used where the same planting material from INFAPRO nursery. Specifically wood density was measured for all saplings at the final harvest, after almost two years of growth, using approximately 30 cm of the lower stem and following the protocols outlined by Chave (2005). Seeds were collected during a masting event in 2010 for two experiments conducted at the site (O'Brien *et al.* 2013; 2014). A total of 1887 seeds were collected,

(range: 49 - 137 per species), oven dried and individually weighed.

Data analysis

Recent studies have shown that accounting for size differences among species can change our interpretation of growth rate data (Turnbull *et al.* 2008; Hautier *et al.* 2010; Rees *et al.* 2010; Turnbull *et al.* 2012; Philipson *et al.* 2012). Put simply, because relative growth rates generally decline as organisms grow comparisons of RGR calculated for species of different sizes risk attributing differences in growth rate due to size with those due to intrinsic species differences. Therefore, we allowed for the estimation of growth rates at a specific size by fitting a curve to multiple diameter measurements through time. Growth was modelled as a power law, following the method described in detail in Philipson *et al.* (2012), where the absolute growth rate is given by,

$$\frac{dM}{dt} = \alpha M^{\beta} \qquad \text{eqn. 1}$$

where α is a growth coefficient, β is the scaling exponent and M is plant size. Equation 1 has the following analytical solution when $\beta \neq 1$:

$$M = \left(M_0^{1-\beta} + \alpha(1-\beta)t\right)^{1/(1-\beta)} \qquad \text{eqn. 2}$$

where M_0 is the initial size (more details of the derivation are provided in Philipson *et al.* 2012). A β of zero would indicate constant linear growth not dependent on size, whereas a β of one would indicate exponential growth, with no slowing of growth with size. Note that, equation 1 has a change of form of the solution when $\beta = 1$ (Philipson *et al.* 2012) but in this study β was lower than 1 so this did not apply. Equation 2 was fitted to diameter data by estimating M_0, α and β using non-linear mixed-effects models. In order to

compare growth rates to mortality rates among species at a common size we then extracted the parameters from the fitted model and calculated a size-specific relative growth rate (SGR) as:

$$SGR = \alpha M_c^{(\beta - 1)} \quad \text{eqn. 3}$$

where M_c is a common reference size. Because species shared a single value of the scaling exponent β (see results) differences in SGR among species and light in our results are solely due to differences in the growth coefficient, α, and relative rankings do not depend on the choice of the reference size. Note that SGR is still relative growth rate (RGR); the difference is that SGR is an instantaneous RGR at a common reference size, whereas conventional RGR calculations are averages over the growth interval and implicitly assume growth is log-linear (as it is calculated on the log size scale).

Canopy openness was measured at every census interval. The model that gave the best fit to the data used an average of the canopy openness measures. Note that when saplings were substantially taller than the height at which densiometer measurements were recorded, the estimate reflects the light environment created by the tree rather than experienced by the tree. For this reason, we tested various models: the model that fitted best used the average canopy openness until saplings exceeded 160 cm in height, after which the same average value was used.

All analyses were carried out in R 2.15.1 (R Core Team 2012). Growth was analysed using non-linear mixed effects models with the nlme() function in version 3.1-104 of the *nlme* package (Pinheiro *et al.* 2012). The models were parameterised with the substantial dataset of over six thousand diameter

measurements on more than a thousand seedlings. We followed the detailed advice provided in Pinheiro & Bates (2000) for model fitting and simplification. Individual seedling identity was fitted as a random effect so that the full model includes an effect of seedling identity on all three parameters. Further simplification of the random effects was attempted, but not possible, i.e. all three parameters were allowed to vary between individuals. We identified the most parsimonious model (fitted using maximum likelihood) based on minimizing Schwarz's (1978) Bayesian Information Criteria (BIC). Models with a BIC of more than 2 points lower were considered better. Species (a factor with a level for each species) and canopy openness (continuous) were treated as fixed effects. We fitted both canopy openness and log canopy openness, but models with log canopy openness were always preferred (as judged using BIC). In the most parsimonious model, α varied with species and with the log of average canopy openness while there was a common value of β and M_0 for all species and canopy openness. The diameter measures were not log transformed and therefore the initial residuals were strongly heteroscedastic. To account for heteroscedasticity, we allowed a unique variance for each species using the *varIdent* function with the *weights* argument in *nlme*. Models were compared when they were fitted with maximum likelihood (ML), but all parameter estimates were taken from the final models fitted using restricted maximum likelihood (REML) as recommended by Pinheiro & Bates (2000). Mixed-effects Models do not report a traditional R^2; therefore pseudo-R^2 was calculated using the squared correlation of fitted and observed values. All models were checked using both plots of the predictions against the raw data and plots of the residuals against the fitted values. Models that had patterns in

348 the residuals, or produced very poor fits to the data were discarded. All
349 models that had sensible predictions and residuals that met with model
350 assumptions were compared using BIC.
351 Mortality data was analysed using generalized linear mixed effects
352 models with the glmer() function in version 0.999999-0 of the lme4 package
353 (Bates, Maechler & Bolker 2013). We predicted the probability of mortality of
354 seedlings given their diameter, species and the canopy openness assuming a
355 binomial error distribution and a complementary log-log link. The intercepts
356 were allowed to vary for both individual seedling and measurement in time as
357 normally distributed random effects (random intercept model). Irregularly
358 spaced census intervals necessitated an offset using log-transformed time
359 since the previous census which produces parameter estimates scaled in
360 units of years rather than census intervals (Barker & Press 1997; Egli &
361 Schmid 2001; Bagchi *et al.* 2011).
362 A matrix of Pearson correlation coefficients was calculated for the
363 species-specific estimates of the growth and mortality measures and four key
364 functional traits (wood density, SLA, leaf C:N ratio and seed mass). Significant
365 correlations were then plotted and relationships were further investigated
366 using Standardized Major axis regression using the sma() function in version
367 3.2.6 of the smatr library (Warton *et al.* 2011).
368
369 **RESULTS**
370 Growth
371 Growth varied among species; *Shorea argentifolia,* the fastest growing
372 species, had a growth coefficient intercept, α, of 0.000908 mm mm $^{-1}$ day $^{-1}$

(95% CI: 0.000583 – 0.00142), while for the slowest growing species *Dipterocarpus conformis*, the growth cofficient intercept was α = 0.000427 mm mm $^{-1}$ day $^{-1}$ (95% CI: 0.000328 – 0.000555). Diameter growth, α, increased linearly with log canopy openness with a slope of 0.092 (95% CI: 0.061 – 0.123). Growth rate increased with increasing canopy openness, but there was no statistical interaction between species and log canopy openness (Δ BIC on removing interaction = -99.20), which indicates no clear difference between species in their growth responses to light. Species did not exhibit exponential growth as indicated by the common scaling exponent, β, which for all species and light treatments was estimated at 0.86 (95% CI: 0.77 – 0.94; Fig. 1); a β of zero indicates linear growth, whereas a β of one indicates exponential growth. This suggests that increased self-shading, allocation to structural tissue etc., results in slower growth rates for larger individuals as expected. The diameter growth model explained a large amount of the variation with a Pseudo-R^2 of 0.986. The high value must be interpreted remembering that the model includes random-effects for both among and within species variation (individual level random effects accounts for within species variation).

Mortality

Probabilty of mortality decreased with initial diameter of seedlings, regardless of species ($\beta_{\text{inital diameter}}$ = -0.01; 95% CI: -0.03 – 0.01). After initial size differences were taken into account, there was an effect of both light and species on seedling mortality. The probability of mortality decreased with increasing canopy openness ($\beta_{\text{canopy openness}}$ = -0.11; 95% CI: -0.16 – 0.07).

398 and species had different intercepts in their probabilty of mortality; *Shorea*
399 *argentifolia* had the highest mortality rate of 0.182 year^{-1} (95% CI: 0.050 –
400 0.514) while *Hopea sangal* had the lowest of 0.054 year^{-1} (95% CI: 0.014 –
401 0.185; Fig 2). However there was no statistical interaction between species
402 and canopy openness (Δ BIC on removing interaction = -91.25), indicating
403 minimal evidence for differences among species mortality in reponse to light.
404
405 Growth mortlity trade-off
406 All species responded to light in a similar way in terms of growth and mortality
407 (Fig 1 & Fig 2). Growth was positively correlated with mortality regardless of
408 canopy openness. An increase in diameter growth rate of 0.1 mm mm^{-1} year^{-1}
409 caused a 4.3% increase in probability of mortality year^{-1} ($\beta_{\text{diameter SGR}}$ = 0.433
410 mm mm^{-1} year^{1}; 95% CI: 0.27 – 0.70; Table 2 & Fig 3). The fact that both
411 growth and mortality differ among species but without interactions between
412 species and light, indicates that a general growth mortality trade-off is evident
413 across all light environments. This suggests that the trade-off is driven by
414 intrinsic species differences rather than differential species responses to light.
415 *Shorea argentifolia,* for example, exhibited the highest probability of mortality
416 per year and the highest growth rate. In contrast, *Parashorea tomentella*
417 consistently had one of the lowest growth and mortality rates, regardless of
418 canopy openness (Fig 1 & 2).
419
420 Correlations among functional traits and growth and mortality rates
421 Wood density was negatively correlated with growth and mortality (Table 2,
422 Figure 4). No other functional traits were significantly correlated with growth

and mortality rates, or with any other functional trait (Table 2). The dataset includes only 15 species and so has limited power for predicting these bivariate relationships, nevertheless there are some correlations that are not significant and yet more than 40% of the variance was explained by the relationship. For example, leaf C:N was negatively correlated with SGR and SLA, and positively correlated with wood density. These correlations were not statistically significant at the level of $P < 0.05$ with our sample sizes but may still be biologically meaningful. Seed mass and SLA were not correlated with either growth or mortality rates, but were negatively correlated with each other.

Discussion

We found that growth increased with light for all species but that each species had different intrinsic growth rates. Interestingly, we found no evidence that species grew differently in response to light; species either grew rapidly or slowly relative to the rest regardless of light environment. Additionally, mortality decreased with increasing light, and species had different intrinsic mortality rates. Species did not respond differently to light, but species that showed high mortality in the shade also had high mortality in higher light conditions. Species that had high growth rates had high mortality rates indicating a strong trade-off between growth and mortality. Wood density was the only trait correlated with both growth and mortality, indicating that wood density could be a useful predictor of growth and mortality rates.

Growth

448 Growth of all species responded positively to increasing light. There is
449 no evidence that species responded differently to light but instead some
450 species simply out-performed others under all light conditions (Fig. 1). This
451 result is in contrast to many studies which have reported variation species
452 growth responses to light (Sack & Grubb 2001; 2003; Baltzer & Thomas 2007;
453 Philipson *et al.* 2012). However, many of the studies that show crossovers in
454 rank among some species, come from shade house studies (Sack & Grubb
455 2001; 2003; Philipson *et al.* 2012). The data from this field-based study
456 supports no crossovers at all – rather a complete positive correlation between
457 growth in all light environments. The apparently contradictory results may be
458 due, in part, to the controlled conditions of shade-houses, which tend-to allow
459 greater sensitivity in detecting differences in growth rates. In addition some of
460 these crossovers may be due to size effects - which we have controlled for in
461 our study. Moreover, there have been strong arguments that studies reporting
462 crossovers are not supported statistically (Kitajima & Bolker 2003; Kitajima &
463 Poorter 2008). The result that sapling growth rates in our field study showed
464 no partitioning for light supports the argument that crossovers in growth rates
465 are not statistically supported.
466 Our results were supported by a study by Bloor and Grubb (2003) that
467 investigated seedling growth rates of 15 shade-tolerant tropical trees in
468 Australia. They showed a strong positive correlation between growth rates in
469 high and low light, and only a very limited number of crossovers in rank
470 growth performance. Most studies that have tried to quantify the growth
471 response of tropical trees to light have focused on a small number of species
472 at the seedling or sapling stage (Poorter 1999; Dalling, Winter & Hubbell

2004). However, Ruger *et al* (2011a) used a hierarchical Bayesian approach to disentangle the effects of light and size on growth of a large number of tree species in Panama. Their results indicate that growth in low- and high-light environments were highly correlated across species. Furthermore, they found little evidence for light gradient partitioning in terms of growth rates among species. In combination these studies support our findings that within a phylogenetically constrained functional group, there is minimal evidence that species specialize on particular light conditions. Instead, a single growth hierarchy exists across all light environments, suggesting a general trade-off with between growth and mortality among closely related species.

Mortality

Mortality rates differed substantially among species, and across all species mortality rates consistently decreased with increasing canopy openness (Fig. 2). The response to light was the same for all species. This reflects the patterns seen in growth responses to light (i.e that species appear to have intrinsic differences in their mortality rates rather than differential responses to light). Bloor & Grubb (2003) also found no interaction among species and light for mortality in shade-tolerant species. Kunstler *et al.* (2009) accounted for size differences in their mortality models and found a strong effect of seedling size on the interaction between light availability and species identity (i.e. smaller seedlings had a stronger light-species interaction than larger ones). Therefore, the large size of our saplings may explain the lack of a species-light interaction (Kunstler *et al.* 2009). Although our results cannot elucidate the potential importance of ontengenic shifts in species rank

crossovers, it is clearly the next step to understanding the complex development of understorey seedling communities (Baraloto *et al.* 2005).

Growth mortality trade-off

There was a positive relationship between mean growth rate and mean mortality rate (Fig. 3). A trade-off between growth in high light and mortality in low light has been reported in many studies and is a recognized process in tropical forests (Kitajima 1994; Davies 2001; Dalling & Hubbell 2002; Kitajima & Bolker 2003; Poorter & Arets 2003; Baraloto *et al.* 2005; Dent & Burslem 2009). The trade-off between growth in high light and mortality in low light has previously been presented as dependent on species-specific interactions with light, such that some species have high growth rates in the light and increased mortality in the shade, rather than consistently high mean growth rates and high mortality per se (Baraloto *et al.* 2005; Dent & Burslem 2009). However, there was no evidence for a statistical interaction between species and light for either growth or mortality in our analysis. The growth mortality trade-off we report is therefore evident in all light environments (Fig. 3), and not dependent on species crossing over (i.e the species all respond similarly to light). A limited number of other studies have also shown a trade-off in growth and mortality rates in specific light environments rather than only for the typical extremes. For example, Kitajima (1994) reported a trade-off between growth and mortality in low-light for 15 tree species from Barro Colorado Island, Panama, and Wright *et al.* (2010) reported a growth mortality trade-off for average growth rates and overall mortality rates across 103 woody plant species from the same site. However, Wright *et al*. (2010) noted

that the trade-off was strongest when growth rates of the fastest growing individuals and mortality rates of the slowest growing were evaluated. Our results suggest that it is intrinsic differences in species mortality or growth rates that explain this trade-off rather than plastic responses, drawing focus to differences in species traits, rather than to their response to the environment.

Trade-offs purely in fitness components involve species with lower mortality exhibiting lower maximum relative growth rates (Latham 1992; Kitajima & Bolker 2003; Baraloto *et al.* 2005). However, the more commonly observed trade-off between high mortality in low light and rapid growth in high light illustrates an interaction between fitness component trade-offs and microhabitat trade-offs, where fitness component trade-offs are only seen when microhabitat extremes are compared (Baraloto *et al.* 2005). This can be generalized as a trade-off between low mortality at low resource availability versus high growth at high resource availability which then promotes coexistence in heterogeneous environments (Wright *et al.* 2010). In support of this, studies have reported that availability of below-ground resources influences the strength of the trade-off between mortality in low light and rapid growth in high light with maximum growth trading off against mortality in the most stressful environment (for example low light and low soil nutrients; Baraloto *et al.* 2005; Dent & Burslem 2009). In contrast, our results indicate a fitness component trade-off between growth and mortality in all light environments, independent of microhabitat trade-offs.

This unique result may be due to a number of factors including the more stressful environment of the logged forest (such as higher temperature, drier soil and lower nutrients); the extended time frame of this study; the fact

548 that it was conducted in situ rather than in a controlled environment; our use
549 of conservative mixed effects models; the method or estimating growth and
550 mortality independent of size effects; and the fact that we used only closely
551 related tree species from within the shade-tolerant functional group. In support
552 of the importance of long-term studies, Sack & Grubb (2001) examined a
553 number of studies focusing on crossovers in species growth performance and
554 illustrate that short-term studies do not adequately represent the processes of
555 long-term natural establishment. Longer time periods can dilute the effect of
556 differences in initial size – explaining contradictory results seen in the
557 literature. We followed the growth and mortality of saplings for 8 years,
558 representing a substantial fraction of the establishment phase. The
559 importance of controlling for size-differences in analysing mortality data was
560 highlighted by both Kunstler *et al.* (2009) and Ruger *et al.* (2011b) – and this
561 may also account for some of the differences between previously published
562 studies and the results that we present here.
563
564 *Wood Density*
565 Physical damage to seedlings from tree falls and herbivory may be
566 important in maintaining the growth and mortality trade-off in forest
567 environments (King *et al.* 2006b; Paine *et al.* 2012). Seedlings can be
568 damaged in both forest gaps and understory sites and so having defense
569 traits, particularly tough wood (King, Davies & Noor 2006a), well defended
570 leaves (Coley & Barone 1996; Alvarez-Clare & Kitajima 2007) and
571 carbohydrate storage (Myers & Kitajima 2007; O'Brien *et al.* 2014), may
572 decrease the likelihood of mortality in all forest environments. We found that

both growth and mortality were strongly negatively correlated with wood density. This result is similar to that reported by Wright *et al.* (2010) who found wood density was significantly correlated with growth and mortality. However Ruger *et al.* (2012) showed that intrinsic growth rates, light response and size response were all related to wood density, suggesting that wood density may represent a complex suite of trait interactions. Moreover, recent work applying engineering theory, showed that greater strength for a given investment could be achieved by a larger diameter – which has questioned the ecological value of high wood density (Anten 2010; Larjavaara & Muller-Landau 2010). We did not find a correlation between growth or mortality and any of the other traits measured, suggesting that wood density may still be an important trait involved in the growth mortality trade-off. Future work should focus on the relationship among size, allocation, growth and wood traits.

A detailed understanding of the mechanisms allowing species coexistence in these diverse tropical forests is far from complete but we finish by briefly discussing some potential implications of our results in light of the existing literature. Our results are not consistent with rank crossovers in the performance of species under different light conditions as a mechanism promoting species coexistence within this single functional group of shade-tolerant canopy species. Instead, we show a general (light independent) trade off between growth and mortality that is consistent across the light gradient. In real terms, for a growth rate increase of 0.1 mm mm^{-1} $year^{-1}$, the annual mortality increases by 4.3%. Ultimately, species that have such higher mortality rates will need to produce more offspring to maintain their population growth rates, yet investment into offspring may trade-off with characteristics at

598 other ontogenic stages (Baraloto *et al.* 2005) such as seedling and sapling
599 mortality rates. The long time-scale and novel size-standardized analysis we
600 use provides new insights into seedling dynamics and indicate that even
601 closely related species in one functional group have pronounced differences
602 in growth and mortality strategies. To what degree these different strategies
603 may help to explain the maintenance of coexistence in these highly diverse
604 tropical forests is unclear. Nevertheless, understanding the role of light on
605 species growth and mortality will allow us to address other potential niche
606 axes more directly; especially as climate change alters resource and water
607 availability.
608 In conclusion, our analysis of the growth and mortality of enrichment
609 planted seedlings of 15 species of dipterocarp over 8 years provides no clear
610 support for species-specific responses to varying light conditions. Instead, our
611 results support a general trade off between growth and mortality across the
612 light gradient from deeply-shaded understory to large lighter gap conditions.
613 This trade off appears to be associated with wood density such that trees that
614 have denser wood have lower diameter growth rates and lower mortality.
615

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618 especially the site manager Philip Ulok, without whom none of this work would
619 be possible. An earlier version of this manuscript has been greatly improved
620 by comments from Kaoru Kitajima and Lourens Poorter. The SBE is part of
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623

624 **Author Contributions**

625 Conceived and designed the study: CDP, GR, RN, AH. Collected the data:

626 CDP, SP, PS, MJO, DD. Analysed the data: CDP, MJO, DHD, AH. Wrote the

627 paper: CDP, DHD, MJO, GR, JC, AH. Local collaborator: RN.

628

629 **Data Accessibility.**

630 All data used in this manuscript are present in the manuscript and its
631 supporting information.
632

633 **Formatted References Link**

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Genus	Species	**Abundance and distribution**
Dryobalanops	*lanceolata*	Widespread on fertile soils, abundant on undulating land, to 700 m
Dipterocarpus	*conformis*	Rare, hill dipterocarp forest, clay-rich soils, below 800 m
Hopea	*sangal*	Often on or near river banks in low country and to 500 m
Parashorea	*tomentella*	Common on flat to rolling hills below 200 m
Parashorea	*malaanonan*	Local on clay-rich soil, rarely on riverbanks, on ridges in mountains to 1350 m
Shorea	*beccariana*	Common, lowlands and dry ridges to 1350 m
Shorea	*argentifolia*	Locally frequent on ridges, hillsides and valleys, usually below 600 m
Shorea	*faguetiana*	Low hills and particularly ridge tops at 150-700 m, occasionally to 1000 m
Shorea	*gibbosa*	Locally common on the most fertile clay-loam soils on undulating land and river banks to 650 m
Shorea	*johorensis*	Very common on well-drained fertile soils below 600 m
Shorea	*leprosula*	Widespread, fast-growing emergent, common below 700 m
Shorea	*macroptera*	Common, sandy clay soils on low hills to 600 m
Shorea	*ovalis*	Scattered, usually in moist places in valleys and low-lying ground, occasionally ultrabasics, to 500 m
Shorea	*parvifolia*	Perhaps the commonest dipterocarp, on clay soils on hills below 800 m
Shorea	*macrophylla*	Locally abundant on periodically flooded alluvium and near rivers, uncommon on hillsides, below 600 m

Table 1.

	Wood density	Seed Mass	Leaf C:N	SLA	SGR
Wood density					
Seed Mass	-0.33				
Leaf C:N	0.49	0.27			
SLA	0.34	-0.41	-0.39		
SGR	**-0.74****	0.14	-0.50	-0.17	
Mortality	**-0.52***	0.10	-0.13	-0.16	**0.54***

Table 2.

	Wood density	Seed Mass	Leaf C:N	SLA	SGR
Wood density					
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Table 2.

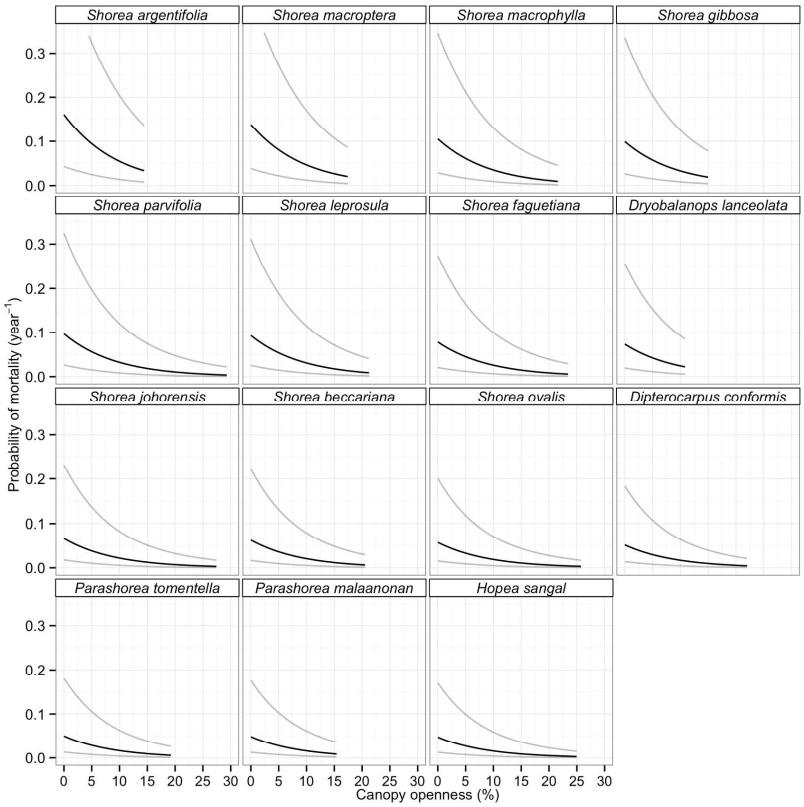
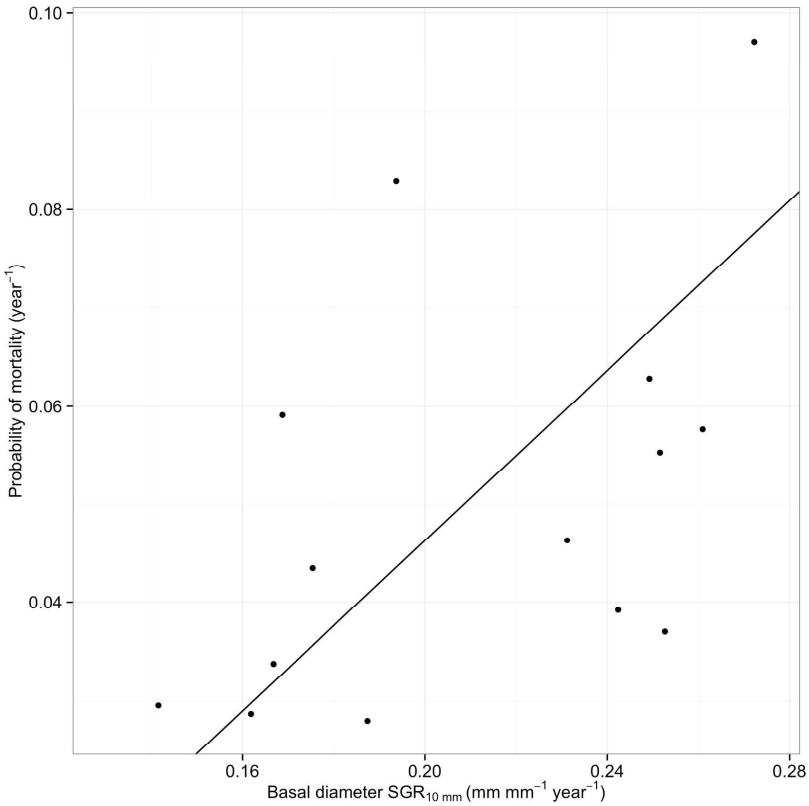

Shorea argentifolia
Shorea macroptera
Shorea macrophylla
Shorea gibbosa
Shorea parvifolia
Shorea leprosula
Shorea faguetiana
Dryobalanops lanceolata
Shorea johorensis
Shorea beccariana
Shorea ovalis
Dipterocarpus conformis
Parashorea tomentella
Parashorea malaanonan
Hopea sangal
Probability of mortality (year^{-1})
0.0
0.1
0.2
0.3
0 5 10 15 20 25 30
Canopy openness (%)

Figure 2



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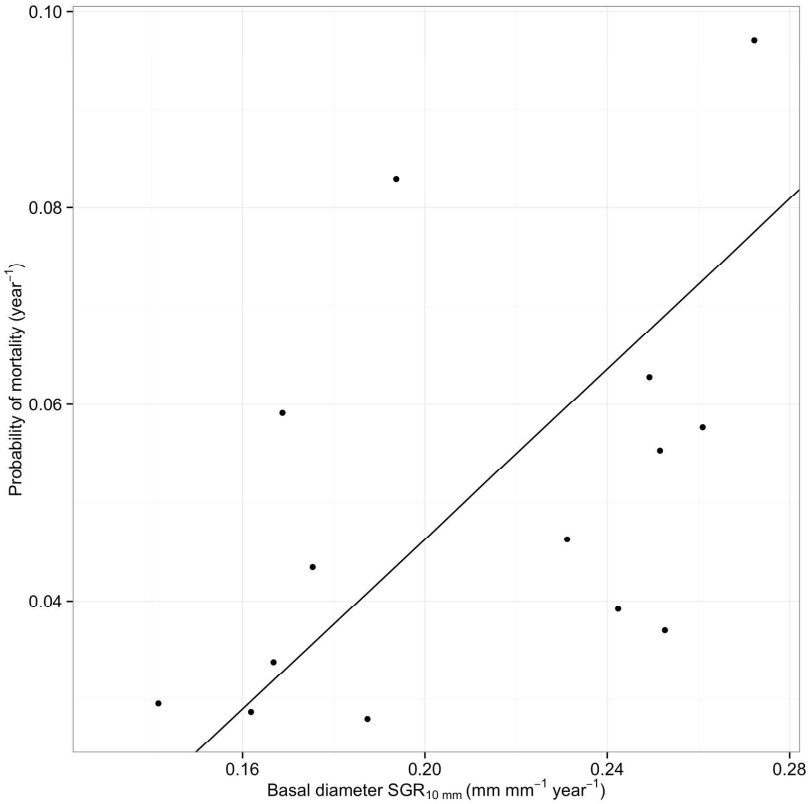
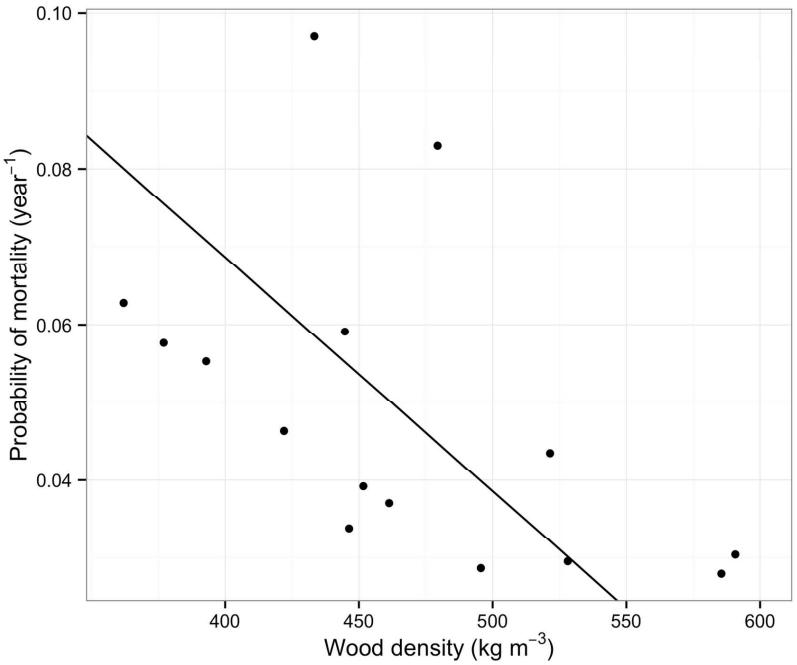
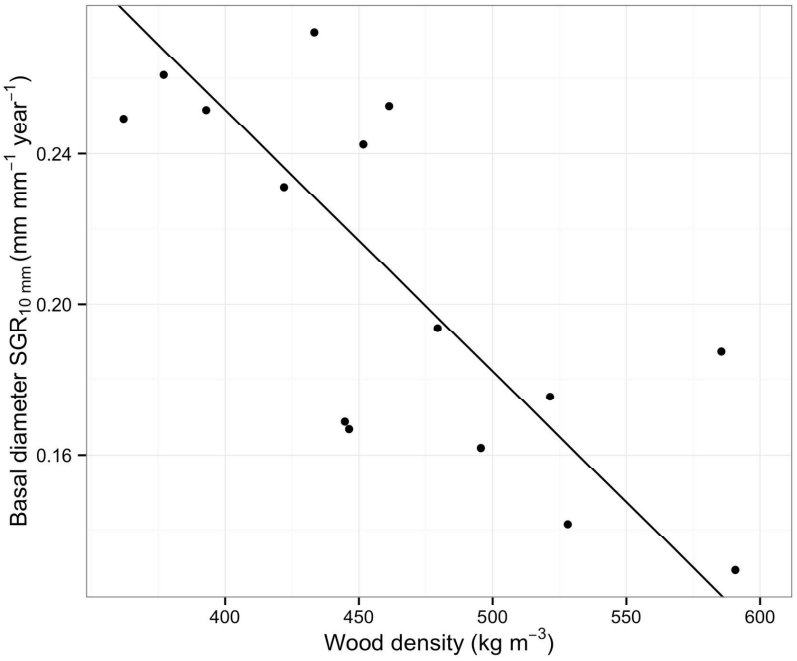


Figure 3.


0.10
0.08
0.06
0.04
Probability of mortality (year^{-1})
400
450
500
550
600
Wood density (kg m^{-3})


0.24
0.20
0.16
Basal diameter SGR$_{10\ mm}$ (mm mm^{-1} year^{-1})
400
450
500
550
600
Wood density (kg m^{-3})

37

Figure 4

FIGURE LEGENDS

Figure 1.

Modeled basal diameter through time for saplings of 15 Dipterocarp species. Panels are ordered by the fastest growing species (*Shorea argentifolia)* in the top left to the slowest growing species (*Dipterocarpus conformis)* in the bottom right. The diameter growth model explained a large amount of the variation with a Pseudo R^2 =0.986. Predictions are for a mean canopy openness (4.5%) and based on individuals of mean size (6.4 mm diameter) and are thus not confounded by size differences between species and. The error bars are 95% confidence intervals calculated by sampling the parameter estimates 1000 times and fitting the power-law through time for each of the 1000 runs.

Figure 2

Probability of mortality estimated at a common size in response to percentage of canopy openness. Panels are ordered by species mortality with the species with the highest mortality in the shade in the top left (*Shorea argentifolia)* and the species with the lowest mortality in the bottom right (*Hopea sangal).* Estimates are only plotted for the range of canopy openness observed in the data set for that species. These predictions were generated using a model with no species light interaction, so the response to light is the same for each species. Thus the curve represents a section of a logistic curve, and only the intercept and the range of data determine species differences.

Figure 3.

Mean probability of mortality plotted against growth rate of basal diameter (growth and mortality rates are calculated for 10 mm diameter seedlings) for 15 Dipterocarp species. Line indicates Standardized Major Axis regression. $R^2 = 0.30$, $P = 0.036$.

Figure 4

The relationships between species wood density and mean annual probability of mortality ($R^2 = 0.27$, $P < 0.047$; top panel), and species wood density and mean basal diameter growth rate ($R^2 = 0.55$, $P < 0.001$; bottom panel; growth and mortality rates are calculated for 10mm diameter seedlings) for 15 Dipterocarp species. Lines indicate Standardized Major Axis regression.

Table 1.

Abundance and distribution of the Dipterocarp species used in this study. Data on abundance and distribution were obtained from Meijer & Wood (1964), Ashton (1982) and Newman et al. (1999).

Table 2

Pearson's correlation coefficients for all pairwise combinations of `growth and mortality` rates and four functional traits. Significant correlations are indicated in bold and with one asterisk indicating significance at <0.05, and two asterisks indicating significance at <0.01.

Sustainable development in Malaysia, how a green economy could work - Pusaka akar

We in Malaysia have been extremely fortunate to be able to live in one of the most biodiverse regions in the world. Our forests are one of the most diverse systems that the planet has ever seen, with as much as 300 species of trees able to occur within a single hectare of forest. This figure far exceeds many other nations; as an example, the entire United Kingdom only has a total of roughly 30 odd species of native trees. Forests and biodiversity contribute tremendously to our wellbeing. Trees consume carbon dioxide for their own growth and in return expel much needed oxygen. Forests as a whole contribute to regional maintenance of weather systems, are important for watershed protection and control erosion. Not only are forests important to us but they provide refuge to up to 50 percent of the worlds species. However, with an ever growing human population on planet earth, forests are being overexploited for its valuable resources at rates which they can hardly keep up with, and within time replaced in order to satisfy our global demand for vegetable oils.

We currently value forests not for the services they provide but for their economic commodities - Timber. From the early 1950s the extraction of timber was small and were restricted to the capabilities of people to move these giants of the forests with the aid of having rivers nearby. The use of rivers had also restricted what people could harvest. Not all trees float, and because of their high densities only the lightest of the timber could be transported with this method. The mechanization of timber extraction from the 1970s onwards led to unprecedented extraction rates which resulted in the removal of trees in volumes larger then what could be sustained naturally. What we have failed to understand is that these forests are different and fragile, they are different in the sense of their reproductive and regeneration biology. As an example, in pine forests throughout the world, you can easily clear a forest and remove its timber with the use of tractors and in a year, the next generation of pine trees can be seen emerging. However in our forests, seeds don’t have the chance to sit as a seed. They germinate almost instantly when they fall and sit on the forest floor waiting for favorable condition to occur. It is this step which makes these seeds extremely vulnerable and sensitive to logging operations and has not been taken into account when harvesting a forest.

When most of the value has been stripped intensively, these forest then regenerate in a rate too slow for landowners to wait for the next possible logging cycle, and instead move towards converting these lands into plantations which provide lucrative earnings. Plantations now cover a large percentage of land and many of which emerge at the cost of natural forests. We currently have a higher percentage of degraded forests compared to those in pristine state and the battle for conservation now lies in the protection of these degraded forests. The large majority of people assume that once a forests is logged, it is considered to be a wasteland. However these residual forests are still capable of maintaining high levels of diversity. Studies have shown that although almost half the biomass has been lost through timber extractions, up to 75 percent of bird species still reside in these forests years after logging. Heavily damaged forests will maintain as degraded forests for years without the intervention of active restoration. Given human intervention, active rehabilitation will increase the forests vertical structure providing suitable conditions where the remaining 25 percent of species would hopefully recolonize.

These research outcomes have proven that these degraded habitats are still able to sustain healthy populations of small mammals and birds. But what about the megafauna? The larger fauna of our nation which includes elephants, tigers, tapirs and orangutans in Borneo all require vast amounts of habitat in order to maintain a healthy population. However with forests being quickly separated from one another their populations are slowly losing genetic diversity and are constantly subjected to inbreeding. Larger mammals such as elephants in North-east Borneo, Sabah, will risk being exposed to human conflict and venture out into un-forested regions in search for other patches of forests to sustain themselves. The need to be able to live along side our natural heritage remains an important task for Malaysia today. It is however not extremely challenging. Populations of humans and wildlife can coexist in the same region if enough planning is taken into account while designing our future nation. Consideration for larger fauna must be taken to account and designing wildlife corridors are of great importance for providing connectivity between fragmented forest are extremely vital for the future maintenance of our wildlife.

The vast amount of plantations are here to stay and as global markets continuously demand vegetable oils which are used in various industries, they will remain to be part of the landscape. Future efforts should be

focused on how to best utilize land already cleared so that they can support productive activities. Solutions on how to live sustainably must be realistic and not over idealistic, which should depend on new conservation policy built on principles of the sustainable use of forests and their surroundings. Not only should these forests be sustainably managed, but the rehabilitation of degraded forests and their future protection remains the key for securing rainforests for future generations to come. What is needed is to integrate these new environments where wildlife can still exist and thrive. Integrating wildlife corridors in order to improve habitat connectivity and reduce forest fragments are only part of the picture. These new structures could also be integrated in order to provide habitat for the smaller species of wildlife and integrate these systems with multiple industries where more then one crop or agriculture can benefit from it. Having cattle roaming or planting shade tolerant crops such as coffee in the understory layers of palm oil plantations are extremely beneficial use of space. However what truly needs to be reduced is the further plantation conversion of natural forests and turn to alternative agricultural lands which have in recent times lost agricultural interest such as rubber plantations. By the increase of productivity in existing agricultural systems and increasing gains on cleared lands we can reduce the need to clear additional forests.

In the past, traditional approaches to rainforest preservation have failed. Setting aside and 'fencing off' forests from the use of rural communities have not proven to work efficiently in developing countries. In order to have forests maintained as a functional ecosystem we have to show that they are able to provide economic benefits standing rather then felled. Conservation efforts need to be self sufficient and sustained for the longterm preservation of these biodiverse lands and not only must they be able to support wildlife, but also the communities they surround. Having ecotourism incorporated into parks can not only fund their existence through entrance fees but they also provide employment opportunities; they will need local guides, crafts workers and also a range of services that any hotel would require. Other future methods included carbon offsetting schemes for the preservation and capture of atmospheric carbon dioxide has in recent times increased the value of these systems by placing monetary values on these trees for the carbon they store, and in the times ahead will play a crucial role in keeping these forested areas as they are. Finally, engaging corporations to adopt reforestation schemes can play a major role. Large corporations are often driven by marketing-driven interests and their involvement in conservation has and will have large contributions for

the environment.

A simple straight forward plan on how Malaysia could sustainably develop will not be easy. The future holds tough choices ahead and we must now gather experts locally and globally who are working on these issues. Only once all these issues have been addressed and displayed on a table can decisions be made on what the future steps should be. The total exclusion of people from these lands are not feasible and the development of multi use reserves must be sustainably developed. The majority of forests that now exist are not entirely protected and in the state which they used to be. Further restoration of these forests and the further implementation of policy to better manage and conserve these forests are among the first steps we need to start taking in order to rise as a sustainable nation.

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